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HEMIZONIA CONGESTA
A GENETIC, ECOLOGIC, AND TAXONOMIC STUDY OF THE HAY-FIELD TARWEEDS

BY
ERNEST BROWN BABCOCK
AND
HARVEY MONROE HALL

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ERNEST BROWN BABCOCK AND HARVEY MONROE HALL

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INTRODUCTION

The present study is a contribution to knowledge of the phylogeny of a small but polymorphous group of Compositae. It was hoped that, by adding detailed garden experiments to the methods usually employed in taxonomy, light would be thrown on the relationships existing within the group, which in turn would facilitate their classification. These experiments were in part ecologic, especially the growing of various forms under uniform conditions. They were also in part genetic in that they involved hybridization of some of the distinct forms found in nature with comparison of first, second, and backcross hybrid generations; also, within two of the minor groups, the selection of biotypes, establishment of inbred strains, and genetic analysis of certain character differences. In addition to the above,

much attention has been given to geographic distribution and field observations as well as to variation, the response to ecologic factors, and the statistical method for testing the value of certain taxonomic criteria.

The study is in itself an experiment to test the value of different methods in taxonomy and the possibility of combining the results obtained by these different methods in an attack upon a problem in phylogeny. There is also a secondary interest in the strictly genetic results secured. But the chief consideration is the advantage of combining the taxonomic and genetic viewpoints in the solution of a problem of this kind. Such a combined effort should not only gain more evidence as to relationships, but should also aid in determining the practicable limits of species and subspecies; for both taxonomists and geneticists have an immediate interest in these concepts. The final solution of the origin of species will come only through the union of the genetic and the taxonomic viewpoints. Consequently there must be taken into account evidence from every possible source, including genetic studies, experimental morphology, cytology, physiology, and the studies, as well, of the field taxonomist, who is primarily interested in the grouping of variads into larger and larger assemblages which at some stage become actually discontinuous as regards numerous characters. The significance of geographic distribution and of isolation in space and time must be appreciated, as well as the bearing of degree of interfertility and the characteristics of the hybrid offspring.

The taxonomic studies were begun in 1912 by Hall, who also started the experiments of an ecologic nature, the Botanic Garden of the University of California being utilized for this purpose. The genetic experiments, made by Babcock, were begun in 1915, the same facilities being used for the first garden cultures and the breeding garden of the Division of Genetics for all succeeding generations. Because of the numerous characters involved and the almost prohibitive cost, not all of the forms here discussed were subjected to genetic analysis. But the results obtained with certain forms suggest what may be expected elsewhere within the group as to genetic behavior. The general outcome of these experiments has been to strengthen considerably the other evidence indicating that the various forms in question, although differing in many genetic factors, are really so close phylogenetically that they should not be treated as distinct species.

The group of forms here included in one collective species has been variously considered by earlier botanists. The first mention of any of them was in 1836, when DeCandolle described *congesta* as the first species under his new genus, *Hemizonia*, and this was followed on the same page but in a different section by a characterization of *H. luzulaefolia*. Although DeCandolle's sections have since been shown to be based upon erroneous observations and of no moment, this arrangement indicates that he conceived of these two forms as entirely distinct. Then followed at intervals descriptions of *sericea* by Hooker and Arnot, *rudis* by Bentham, *fragarioides* by Kellogg, and *lutescens* and *Clevelandi* by Greene; *fragarioides* and *lutescens* being classed as varieties of *luzulaefolia*.

When Gray came to the group, in his treatment for the Synoptical Flora in 1884, he reduced this assemblage to three species, *congesta*, *luzulaefolia*, and *Clevelandi*. Later writers have followed Gray's treatment with little deviation. Only two species have since been proposed, *citrina* by Greene and *grandiflora* by Abrams.

It is now found that not only must these last two be included in certain subspecies of *congesta*, for reasons to be stated in the taxonomic part of this paper, but that *luzulaefolia* and *Clevelandi*, also, are to be considered as but subspecies. This is due not so much to a shifting in species concepts as to the much greater abundance of material, to field studies, and to results obtained from experimental and cytological data. The only specimens of typical *congesta* available to Gray consisted of two fragments of the original collection and one other from a plant grown from seed of this same collection. Later students of the group have had scarcely more. Recent explorations, however, have resulted in assembling a large series of specimens including many of typical *congesta*, so that the intimate connection of this form with the others can now be demonstrated. With all of the evidence now available before them, the present authors feel that all these forms together comprise only one inclusive species and that the natural divergent manifestations within this species are best treated as subspecies. Of these latter, six are definitely recognized, although each is composed of innumerable forms, some of which are genetic and can be maintained by selection.

THE SPECIES AND SUBSPECIES CONCEPTS

Phylogeny the basis for classification.—Phylogeny must be taken as the guiding principle in taxonomic study. With this in mind, an examination has been made of all of the available forms of this group of tarweeds with a view to determining their relationships to one another, that is, the route over which each has traveled in its evolution from the common ancestral type. Through the use of all available evidence there has thus been built up a picture of the evolutionary tree with each of the present day recognizable forms as the ultimate twigs, all more or less definitely connected to a central stock.

The most important part of any taxonomic investigation is the determination of these relationships, but the matter of their expression in a readily intelligible and usable form is also to be considered. This expression for the present group is attempted, a little farther on, by the use of a key and a diagram of phylogenies. But it is expected that the names themselves shall express something of this relationship, and it is partly for this reason that the six most outstanding forms—the six main twigs of the evolutionary branch—are here treated as subspecies rather than as species, for this at once indicates their derivation from a common stock.

Species and subspecies are more than concepts.—It should here be noted that from this phylogenetic point of view each subspecies is a real entity, just as much as every true species and every branch of an actual tree is an entity, for it is composed of all those organisms, past and present, that have arisen from one particular portion of the ancestral plexus. Any taxonomic unit is a concept only in the sense that it can be expanded or contracted to include either more or less of the evolutionary branch. Thus the question as to how large or how small a species should be, that is, whether it should include a large number of natural divergent strains or whether these should be set off as separate species, becomes one of convenience or usability, and is not to be compared in importance with the much more fundamental consideration of its naturalness and relationships.

Large versus small species.—In the present instance the authors are confronted with a choice between (*a*) the recognition of a large number of very 'small' species impossible to delimit because of intermediate forms, and (*b*) the assembling of a large number of variations into one inclusive or 'large' species, well separated both morpho-

logically and phylogenetically (as far as existing forms are concerned) from anything else in the genus. An intermediate course, such as that attempted by earlier workers on the group, seems entirely illogical and misleading.

The present writers earnestly desired, in the interest of stability, to follow a middle course; and so they attempted to conserve as species such well-known forms as *congesta, luzulaefolia,* and *Clevelandi.* But this hope is now abandoned, for it is seen that such a method arbitrarily breaks a complete network of forms into several more or less convenient portions. It is unlikely that the more conservative of the earlier students of the group would have maintained more than one species if they had been confronted with the wealth of material now available and with the facts since assembled from field and garden experiment. If absence of intergradation, in the usual taxonomic sense, is set up as a specific criterion, then only one species is involved; for, as is shown in the statistical data and the taxonomic treatment, each form exhibits an overlapping of one or more of its neighbors in all of its characters; nowhere in the whole series is a hiatus to be found.

On the basis of available cytological evidence these forms would all belong to one species. With the assistance of Dr. Margaret C. Mann, chromosome counts were obtained of three of the subspecies, namely, *typica, lutescens,* and *luzulaefolia.* These were made by Belling's method of examining living pollen-mother-cells at the metaphase or early anaphase stage of the heterotypic or homotypic division. In each case there were clearly 12 chromosomes in the haploid, so that the somatic number for these three forms is 24. Similar material, which happened to be available, from *H. corymbosa* (DC.) T. and G., a distinct species, showed only 10 pairs, making 20 in the diploid. These data, although very limited, are consistent with all the other evidence and tend to confirm the conclusion that the forms under investigation comprise a single species.

As viewed from the standpoint of genetics, each of the units thus far characterized by the taxonomist seems to consist entirely of heterozygous plants, while many intermediate variations, these also heterozygous, have been found. This fact has been definitely determined for the forms known as *congesta, rudis, citrina,* and *lutescens,* and field observations suggest that a similar condition holds for the remaining forms. Such heterozygosity necessarily results from the fact that the individual plant is self-sterile in this species, so that

every viable seed results from cross-fertilization. By selecting pairs of similar plants in the first garden culture, however, and crossing sibs (brothers and sisters) for one or two generations, it was possible to establish fairly uniform strains. Most of these strains remained fairly true to type for the characters noted and would doubtless have become more uniform if inbreeding could have been continued, but there is every reason to believe that, if permitted to run wild again, such strains would revert to the heterozygous state and intercross with other forms.

The number of biotypes possible of isolation in this way is very large. One colony of *lutescens* (*citrina*) yielded 18 segregates in the garden and more could have been derived from the same source. Each selected type was perfectly distinct by at least one recognizable character, and the populations of the resulting strains were, for the most part, rather uniform in the second generation, i.e., after only one brother-sister mating. A few of the selected biotypes, however, proved to be due to heterozygous genotypes and, of course, would not breed true.

When seed is collected from wild plants of the several taxonomic units under consideration and the cultures are grown under uniform garden conditions, there is a noticeable difference in the amount of variation within each culture. The original garden cultures of *rudis* and *lutescens*, which were utilized for genetic experiments, each consisted of several hundred plants; but the *lutescens* culture, derived from a few closely adjacent plants of only one wild colony, was decidedly more variable than the *rudis* culture which was derived from two widely separated colonies and included the progeny of scattered plants. It is therefore not likely that all the forms being considered would yield distinct garden strains in equally large numbers. But if all of the variations were assembled from the whole range of the species and subjected to selection and inbreeding, it is probable that the segregates would number into the thousands. This is predicted both from the large number of variations observed among wild plants and from the fact that the total number of possible combinations of the characters already studied is exceedingly high. A similar conclusion was reached by Clausen (1922) in the case of *Viola tricolor* and *V. arvensis* in which numerous variations are induced by genotypical differences due mainly to frequent crossing between the species. In this case, however, it happens that the two are perhaps properly maintained as species, because the chromosome

numbers are different and two well-defined types are far more frequent than the transition forms.

The assignment of a binomial or even a trinomial to each of the forms possible through segregation would doubtless be frowned upon even by the strongest advocates of the use of 'small species' in taxonomy. The object in discusing them at this juncture is to call attention to their large number and to demonstrate that, because of the numerous combinations of their characters when interbreeding is permitted, there has been developed, even in a wild state, such a network of forms that to cut off any portion of this net as a species is both impracticable and misleading. It seems much more serviceable to designate the ultimate genetic units merely by monomials, letters, or figures when it is found that a designation is desired, as may well be the case in detailed studies in genetics or of uses, ecology, etc. A few of these genetic types as well as some of the more striking ecologic forms are described in the present paper under the heading of Minor Variations.

Species and subspecies as the terms are here employed.—With the foregoing consideration in mind it seems advisable to reserve the category of species for a major grouping well set off phylogenetically from all other species in the genus, and to bring in the subspecies as a subordinate group set off from other subspecies only by lesser but still genetic characters or by various combinations of these. This is essentially the method recently applied by Hall and Clements in their Phylogenetic Method (Hall and Clements, 1923). Thus the subspecies constitutes a more or less definite evolutionary unit, which is itself composed of still smaller units or forms and, on the other hand, unites with other subspecies to constitute a larger natural group, that is, the species.

Considered genetically, the subspecies possesses the same hereditary basis and the same chromosome complex as the remainder of the species, but differs with respect to certain genes. In the case of cross-fertilized species, such as the one under discussion, it is almost inevitable that genotypic differences occur within the subspecies. These make possible the establishment of strains by selection of biotypes followed by inbreeding. They also are responsible for much of the natural variation occuring within the subspecies.

The subspecies is thus placed in the same relation to the species that the subgenus bears to the genus, and like the subgenus it is readily omitted whenever the category is not for the moment of service.

It is partly for this reason that the term 'subspecies' is preferred to 'variety'; also its use is established in zoology, the term is free from the confusing connotations of the horticulturist's 'variety,' and carries, moreover, a somewhat higher value, especially in its phylogenetic significance, than is usually given to the taxonomist's 'variety.'

DEVELOPMENT OF SPECIAL FEATURES

An enumeration of the guiding principles applicable to all problems concerning the phylogeny of any group of organisms has been formulated by Bessey (1914). The authors are in agreement with most of Bessey's dicta and have taken all of them into account in the present study. The following considerations are submitted as supplementary evidence and as more specifically applicable to the problem in hand.

Size and shape of ray-achenes.—The ray-achenes are fairly uniform in the species except that in the subspecies *Clevelandi* the tendency is toward a greater diameter in proportion to length. In other words, they are plumper than in the remaining forms. This tendency has been tested by a statistical study involving the length and breadth of the ray-achenes of all of the forms. The absolute measurements indicate only certain tendencies, with a high degree of overlapping, but when the shape is expressed in the form of a ratio of breadth to length it is found that *Clevelandi* may be differentiated by this character in nearly all instances. As may be seen from table 1 (p. 28), the ratio for this subspecies is 61 to 68 per cent, with the exception of a few collections, in one of which it drops to 57 per cent. In the other subspecies the ratio is usually 50 to 61 per cent, but with occasional specimens running to 65 per cent, especially in *typica*, the form most unlike *Clevelandi* in other respects. That this difference is not entirely a response to the hot and arid climate in which these forms grow is indicated by occasional high ratios in achenes of *typica* of the more humid coast districts, and by the fact that in the other subspecies the higher ratios are not characteristic of plants from within or near the area of *Clevelandi*.

Since the only form with a high breadth to length ratio for the ray-achenes is one which is also unique because of a tendency toward a reduction in the inflorescence, and since the form occupies a somewhat outlying geographic area, it is assumed that this achenial feature is indicative of a modern type.

Shape of cotyledons.—There is a close resemblance in the shape of cotyledons among all the subspecies in which this seedling character has been observed. It happens that in the case of *typica* the cotyledons are more nearly orbicular, while in *lutescens* and *luzulaefolia* they are oblong. Also in crosses between *typica* and *lutescens*, the *typica* cotyledon shape seems to be dominant. But this fact does not necessarily imply that the *typica* cotyledon shape is the more primitive. At any rate, this is only a minor difference such as might be expected among subspecies.

Color of flowers.—The yellow color in the ligules of some of the subspecies is due to a yellow pigment (possibly two) present in the chromoplasts. It is assumed that the presence of this pigment is primitive to its absence. The tendency of many species characterized by colored flowers to produce white-flowered variations is well known. A few cases of the production of colored from white varieties have been reported, but their rarity would be an argument against the development of *lutescens* from *typica*. Moreover, yellow flowers are the rule in nearly all Hemizonias, and indeed almost throughout the tribe of Compositae to which they belong. The genetics of flower color in this species is discussed on page 76.

Tips of the involucral bracts.—Each bract consists of a basal portion which closely invests the achene, and is therefore strongly concave, and a flat, lanceolate tip. In the subspecies *typica* and *calyculata*, this tip is so greatly elongated as compared with the short tips of the other subspecies that it constitutes a specialized feature. It was used by Gray, along with certain tendencies in the pubescence, as of specific value, for he referred to the bracts of typical *congesta* as overtopping the disk. But when a large series of specimens is brought together and subjected to actual measurement, it is found that this character is so variable as to be of only secondary importance. The extent of variation and the amount of overlapping between the various subspecies is brought out in table 1. The tabulation also shows a decided tendency toward an elongation of the bracts and especially of the flat tips in *typica* and *calyculata*, and this tendency is one of the best features whereby to differentiate these from the other subspecies. Since such bracts do not occur elsewhere in the genus, the forms bearing them are looked upon as having been derived from others with ordinary short-tipped bracts. Thus *typica* may or may not have been derived from the *lutescens* branch, but almost certainly the sequence could not have been the other way around,

i.e., *lutescens* with the usual short-tipped bracts could scarcely have been derived from the long-tipped form unless by reversion. This assumption receives support from other considerations, especially flower color and geographic distribution. It should be noted, however, that although long tips do not occur in the immediate relatives of the species they are found in some of the Layias, of the same subtribe of Compositae. This is perhaps a case of parallel development in related groups.

Size of heads.—The heads average larger in forms flowering in spring than in those which mature in the late summer and autumn. Measurements are difficult to make except when fresh material is available, but the length of the involucral bracts may be taken as an index of the size of the whole head. From table 1 it is seen that the average bract length for the genuine spring type of *luzulaefolia* is 5.0 mm.; of the fall flowering or *rudis* type, 4.1 mm. In the case of *lutescens,* the spring or *citrina* type averages 5.4 mm.; the genuine or autumnal type, 5.6 mm. This reversal of the rule is believed to be due to chance because of the small number examined, but it emphasizes the difficulties in using this criterion. The length of the ligules, as measured on fresh flowers, has also been taken as an index of head size. The average of 43 measurements of the spring form of *luzulaefolia,* from various localities, is 10.1 mm. The average of 13 measurements of the autumnal form from Richmond is 9.5 mm. These figures include the length of tube as well as of blade. In garden cultures it was found that seeds gathered in San Mateo County from the large-headed form produced, the following year, plants with heads larger than those of the wild late flowering form, but no larger than those of cultures of the latter growing under apparently identical conditions. In fact, in one bed of the late form, the original seed of which came from Richmond, the heads were larger than in any of the three beds of the spring form. The cultures became impure after the first season, because of crossing, and were therefore discontinued.

The conclusion is that, while the size of head must have a certain genetic basis, yet much of the variation in head size is associated with varying ecologic conditions that obtain at different seasons; the largest heads being produced in the spring and early summer, when growth conditions are at their maximum. On the other hand, certain of the inbred strains isolated during our genetic investigations were characterized by large, showy heads as compared with the general average.

TABLE 1

A STATISTICAL STUDY OF CHARACTERS IN THE SUBSPECIES OF HEMIZONIA CONGESTA

	Herbarium	Bracts of the involucre			Ray-achenes		
		Length of body[a]	Length of tip	Total length	Length[b]	Breadth	Ratio of breadth to length
		mm.	mm.	mm.	mm.	mm.	per cent
Subspecies *a. lutescens:*[c]							
Rodeo Lagoon, Marin Co.[d]	89001 UC	3.0 3.5	3.0 3.2	6.0 6.7	2.6 2.4	1.2 0.9	44 38
Rodeo Lagoon, Marin Co.[d]	89417 UC	3.0 3.5	3.0 1.5	6.0 5.0	3.1 2.9	1.3 1.3	42 45
N. of Bolinas, Marin Co.	197524 UC	4.0 3.2	1.8 2.6	5.8 5.8	2.5 2.4	1.5 1.2	60 50
S. of Petaluma	194215 UC	3.0 3.0	1.6 1.2	4.6 4.2	2.6 2.6	1.6 1.4	61 53
Near Tocaloma, N. Marin Co	197514 UC	4.0 3.2	2.1 2.8	6.1 6.0	2.8 3.3	1.5 1.7	54 53
Tiburon Isl., south side	201232 UC	3.0 3.5	2.0 2.5	5.0 6.0	2.8 2.7	1.3 1.5	46 54
Tiburon Isl., south side	193431 UC	3.5 3.0	1.5 2.0	5.0 5.0	2.6 2.7	1.5 1.6	55 57
Marin Co	32739 UC	3.2 3.0	3.0 2.0	6.2 5.0	2.8	1.6	57
Tomales Bay	89003 UC	3.2 3.0	2.0 1.5	5.2 4.5	2.9 2.8	1.6 1.8	53 63
Olema	89004 UC	3.5 4.0	2.8 2.2	6.3 6.2	2.8 2.9	1.6 1.6	56 55
Average		3.3	2.2	5.5	2.8	1.5	53
Subspecies *b. typica:*							
"California" (from type)	Gr	3.0	5.0		3.0		
San Francisco	185666 UC	2.8 3.2	4.0 4.5	6.8 7.7	2.5 2.5	1.5 1.6	60 63
Near San Rafael, Marin Co	197513 UC	3.2 4.0	3.0 4.3	6.2 8.3	2.4 2.4	1.5 1.4	64 60
Near Petaluma	197506 UC	3.0 3.0	3.0 3.0	6.0 6.0	2.7 2.6	1.6 1.5	60 59 57
Near Petaluma	193422 UC	4.1 4.0	4.1 5.0	8.2 9.0	2.5 2.4	1.3 1.4	58 55
Near Petaluma	193421 UC	3.3 3.6	3.7 3.4	7.0 7.0	2.8 2.7	1.5 1.6	51 59
Tomales, Marin Co	89002 UC	4.0 3.0	5.0 3.5	9.0 6.5	2.9 3.0	1.5 1.6	52 53
Verano	89028 UC	2.7	3.2	5.9			
Near Santa Rosa	134571 UC	3.0 2.5	4.5 3.5	7.5 6.0	2.6 2.5	1.7 1.6	65 64
Santa Rosa	65349 UC	4.0 3.1	3.6 2.8	7.6 5.9			
Pudding Cr., Mendocino Co	89000 UC	3.2	3.6	6.8	2.6	1.7	65
Cape Mendocino, Humboldt Co.[e]	204741 UC	3.5 3.6	3.2 4.5	6.7 8.1	2.8 3.3	1.5 1.4	53 43
Average		3.3	3.8	7.1	2.7	1.5	58
Subspecies *c. calyculata:*							
Willits, Mendocino Co.	174169 UC	3.0 4.0	5.2 6.5	8.2 10.5	3.1 3.0	1.7 1.6	55 53
S. side Elk Mt	197533 UC	2.4 2.5	3.8 4.0	6.2 6.5	3.2 3.1	1.7 1.8	53 57
Sulphur Bank, Lake Co.	133119 UC	3.0 3.0	2.7 3.0	5.7 6.0	2.8 2.9	1.6 1.7	56 58
Orr's Springs, Mendocino Co	SF	4.0 3.8	6.0 3.0	10.0 6.8	3.0 3.3	1.7 1.7	56 52
Near Orr's Springs (type)	231427 UC	3.0 3.5	7.0 6.0	10.0 9.5	3.2 3.0	1.7 1.7	53 57
Red Bluff[f]	89024 UC	3.0 2.9	3.5 3.8	6.5 6.7	2.4 2.5	1.7 1.9	71 76
Average		3.2	4.7	7.8	3.0	1.7	58

TABLE 1—(*Continued*)

A Statistical Study of Characters in the Subspecies of Hemizonia congesta

	Herbarium	Bracts of the involucre			Ray-achenes		
		Length of body[a]	Length of tip	Total length	Length[b]	Breadth	Ratio of breadth to length
		mm.	mm.	mm.	mm.	mm.	per cent.
Subspecies *d. luzulaefolia:*[g]							
Crystal Springs, San Mateo Co.	134605 UC	3.0 3.0	2.0 2.2	5.0 5.2	2.4 2.4	1.3 1.2	52 50
Near Millbrae, San Mateo Co.	193427 UC	4.0 3.5	2.5 2.0	6.5 5.5	2.5 2.7	1.4 1.4	52 50
Near Crystal Springs Lake, San Mateo Co.	193424 UC	2.8 3.4	2.0 1.8	4.8 5.2	2.8 2.8	1.6 1.5	53 52
Berkeley, Alameda Co.	32735 UC	3.0 3.0	1.5 1.8	4.5 4.8	2.9	1.5	50
N. Berkeley, Alameda Co.	128325 UC	2.7 3.0	1.6 1.8	4.3 4.8	2.8	1.6	57
Collins, Napa Co.	197531 UC	3.2 3.0	2.0 1.5	5.2 4.5	2.8	1.5	52
Aetna Springs	174177 UC	3.0 2.8	1.0 0.5	4.0 3.3	2.6 2.8	1.5 1.6	58 57
Near Stockton	134557 UC	2.8 2.5	1.2 1.4	4.0 3.9	2.4 2.5	1.3 1.3	54 52
Vanden, Solano Co.	89022 UC	2.5 3.0	0.8 0.8	3.3 3.8	2.6 2.8	1.6 1.7	62 60
Laguna Valley	32731 UC	2.8 2.8	0.6 0.6	3.4 3.4	2.5 2.5	1.5 1.5	59 59
Suisun	128076 UC	2.8 2.8	1.1 1.3	3.9 4.1	2.6 2.5	1.5 1.5	58 60
Richmond, Contra Costa Co.	201236 UC	3.0 3.4	2.2 2.8	5.2 6.2	3.1 3.0	1.6 1.5	49 50
San Pablo, Contra Costa Co.	201230 UC	3.0 2.5	1.8 1.2	4.8 3.7	2.1	1.2	58
Near Williams, Colusa Co.	194238 UC	2.8 2.0	2.7 1.7	5.5 3.7	2.2	1.2	56
Average		2.9	1.6	4.5	2.6	1.5	55
Subspecies *e. Tracyi:*							
Red Mt., N. Mendocino Co.	DS	3.8	3.0	6.8	2.8	1.5	54
Near Blue Rock, Mendocino Co.	DS	3.9 3.6	3.2 3.1	7.1 6.7	3.0 3.0	1.9 1.9	63 63
Bald Mt., Humboldt Co.	180195 UC	3.2 3.2	3.4 3.2	6.6 6.4	2.8	1.6	58
Near Hydesville, Humboldt Co.	180194 UC	3.8 3.2	3.0 2.8	6.8 6.0	2.9 3.0	1.6 1.5	55 50
Mount Pierce, Humboldt Co.	205206 UC	4.0 4.0	2.8 2.8	6.8 6.8	3.2 3.1	1.6 1.6	50 53
Kneeland Prairie, Humboldt Co.	175967 UC	2.8 3.0	2.8 2.6	5.6 5.6	2.4 2.4	1.5 1.5	63 63
Redwood Belt, Humboldt Co.	127611 UC	3.5 3.5	3.5 3.3	7.0 6.8	3.2	1.8	56
Near Buck Mt., Humboldt Co. (type)	176756 UC	3.6 3.5	3.4 3.2	7.0 6.7	3.5 3.5	1.9 1.9	54 54
Kneeland Prairie, Humboldt Co.	205207 UC	3.0 3.2	2.0 2.0	5.0 5.2	3.1 3.2	2.0 1.9	63 59
Laribee Creek, Humboldt Co.	195063 UC	3.6 2.8	3.2 2.8	6.8 5.6	2.8 2.9	1.7 1.7	61 58
Average		3.4	3.0	6.4	3.0	1.7	57

TABLE 1—(*Concluded*)

A Statistical Study of Characters in the Subspecies of Hemizonia congesta

	Herbarium	Bracts of the involucre			Ray-achenes		
		Length of body[a]	Length of tip	Total length	Length[b]	Breadth	Ratio of breadth to length
		mm.	mm.	mm.	mm.	mm.	per cent
Subspecies *f. Clevelandi:*							
Near Healdsburg, Sonoma Co.	75962 UC	3.0 3.0	2.5 2.2	5.5 5.2	2.8 2.9	2.0 1.9	71 64
Calistoga	11950 CI	3.1 2.7	1.6 2.1	4.7 4.8	2.1 2.4	1.4 1.8	67 75
Calistoga	88998 UC	3.0 3.0	2.9 2.8	5.9 5.8	2.9 2.9	1.9 1.8	65 62
Kelsey	88996 UC	2.6	2.4	5.0	2.3	1.3	58
Bradford's, Lake Co.	88999 UC	2.6 3.0	3.0 1.8	5.6 4.8	2.2 2.4	1.3 1.6	59 65
Allen Springs (type collection)	177502 UC	2.4 2.5	2.4 2.0	4.8 4.5	2.2 2.0	1.4 1.3	64 66
Near Lakeport	11935 CI	3.0 3.0	2.7 3.0	5.7 6.0	2.2 2.6	1.5 1.6	68 62
Lakeport	11932 CI	2.4 2.7	2.8 2.1	5.2 4.8	2.1 2.0	1.2 1.3	57 65
Elk Mountain, N. Lake Co.	175978 UC	3.0 2.8	2.8 3.0	5.8 5.8	2.9 2.8	1.7 1.8	59 63
Burnt Ranch, Trinity Co.	205154 UC	2.6 2.8	1.5 1.1	4.1 3.9	2.8 2.8	1.6 1.7	57 61
Near Leesville, Colusa Co.	195406 UC	3.0 3.0	2.9 2.5	5.9 5.5	2.5 2.4	1.5 1.5	60 61
Glenn Co.	179689 UC	2.8 3.0	3.4 4.0	6.2 7.0	2.2 2.2	1.3 1.4	59 64
Bear Creek, Jackson Co., Oreg.	53807 UC	3.3 3.0	3.5 3.5	6.8 6.5	2.9 2.8	1.8 1.9	62 66
Big Butte Creek, Josephine Co., Oreg.	201331 UC	3.0 3.0	2.8 3.0	5.8 6.0	2.5 2.6	1.7 1.8	68 68
Deer Creek, Oreg.	89030 UC	3.1 3.0	2.6 2.5	5.7 5.5	2.6 3.1	1.7 1.9	66 64
Average		2.9	2.6	5.5	2.5	1.6	63

[a] The body is considered as extending to the faint cross-line at base of the flat tip; the body is usually a little longer than the enclosed achene. The achenes measured for this table are not always from the same bracts as those of which the measurements are given.

[b] The length of achene includes the stipe but not the areole.

[c] The last 5 collections tabulated under *lutescens* belong to minor variation 1, an early maturing form sometimes called *H. citrina*.

[d] All localities are in California unless otherwise indicated.

[e] A glandular form described farther on as minor variation 8.

[f] A form with unusually short achenes; further described under minor variation 2.

[g] The last 8 collections tabulated under *luzulaefolia* belong to minor variation 10, a late maturing form sometimes known as *H. rudis*.

Inflorescence.[1]—The racemose and spicate types of inflorescence in this species are modifications from the paniculate type through reduction in the length of the peduncles. This is the opposite of the well-known fact that in general the panicle is a development from the raceme. Reasons for here accepting what may seem to be a reversal of the general theory are that, in all related forms, including those which by all other features are primitive to the species, the inflorescence is paniculate, and that even here we never encounter a true spike; for the 'spikes' themselves are branches of a corymbiform panicle and at least some of the heads are more or less peduncled. It is impossible to conceive of the forms with a so-called spicate inflorescence, for example, *Clevelandi,* as primitive to the others, for this would necessitate, first, their derivation from a paniculate form, there being no other related *Madinae* with spike-like inflorescences, and then the redevelopment of panicles in the other subspecies. On the other hand, with a series of specimens before one it is not difficult to trace the steps whereby the ultimate branches of the panicle (peduncles) have been reduced until the whole inflorescence was simplified into a series of spike-like branches. The reasons for this reduction are only conjectural, but the restriction of the form largely to arid districts where the soil is poor suggests a disturbance in the supply of food and water to the growing parts at the time when the heads and peduncles are forming.[2]

Calyx-like development of the upper leaves.—In two of the forms (*calyculata* and minor variation 2) there is a remarkable assembling of the upper reduced leaves into false whorls, which surround and much overtop the heads. The cause of this is not known, but for reasons to be given later such forms are thought to be of hybrid origin. If this assumption is correct, these forms are of course higher in the evolutionary scale than any of their parents.

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[1] In this paper the term *inflorescence* is taken to mean the arrangement of the heads. In the strict sense, each head is in itself an inflorescence.

[2] Garden experiments carried out since the foregoing was written demonstrate the ease with which the spicate type of inflorescence is converted back into the paniculate, merely by improving the cultural conditions. Seeds gathered from a colony of strictly spicate plants at Calistoga (*Hall 11950*) were grown in good soil at Berkeley and yielded large plants with scattered, paniculate heads. Other plants from the same lot of seed, but grown with less soil moisture, produced heads mostly in spikes but with some subpaniculate inflorescences. Similar results were obtained in cultures grown from seed collected near Lakeport (*Hall 11935*).

Pubescence.—The trichomes are of three main types: (1) long, spreading, non-glandular hairs, giving a villous pubescence; (2) long, appressed, non-glandular hairs, giving a silvery-silky pubescence; (3) short, spreading, gland-tipped hairs, giving a glandular pubescence. The first and third types are present in varying amounts on all plants of the species, and the second type is often present on the lower leaves, the remainder of the herbage being villous and glandular. A striking difference in the appearance of two plants is often due to a difference in the relative number of trichomes of the various sorts, and since all degrees of density are encountered it results that all gradations are found from dark, heavily glandular, and scarcely villous plants, like the common fall flowering form of the subspecies *lusulaefolia*, to the gray, densely soft-villous, and scarcely glandular subspecies *typica*. Since prominent resin glands tipping the trichomes are almost universal in *Hemizonia* and in fact throughout the Madinae, their absence is looked upon as a case of suppression by an inhibiting factor, and the subspecies with few or no glands are considered as derived from strongly glandular forms.

Even less satisfactory is the feature of the silvery-silky pubescence which occurs only on the larger leaves. When all of these are silvered the result is so striking that the character has been given specific value by some, as, for example, in separating *citrina* from *lutescens*. But the difference between a silvery pubescence and a villous one is merely due to differences in the length of the hairs and in the extent to which they are appressed. It is not surprising, therefore, to find all gradations on a single plant, and nearly all degrees are sometimes found on a single leaf. Although it was possible, by selection and inbreeding, to establish strains that were characterized by silvery leaves or, on the other hand, by nearly complete absence of the silvery, appressed pubescence from the leaves, yet there was fluctuation in the amount of pubescence within the strains themselves.

Thus while the relative abundance of the different kinds of pubescence is very useful as indicating tendencies in the subspecies and minor forms, it cannot be used as a satisfactory criterion upon which to establish distinct species.

EVOLUTION OF THE SUBSPECIES

Geographic distribution.—Geographic distribution is to be given serious consideration in all problems of phylogeny. Its bearing in connection with the origin of the subspecies of *Hemizonia congesta* will be taken up as each of these is discussed. It may be interesting here to note that, although this is an endemic group, the results are not in accord with the age and area hypothesis (Willis, 1922). However, because of the small number of forms studied, all of the requirements of this hypothesis are not met. The form which by all other criteria is the most primitive is perhaps also the most limited in distribution, although very plentiful where it occurs. The subspecies (*luzulaefolia*), which is at once the most abundant and widespread, seems to fall about midway in the age scale.

The primitive *lutescens* is centrally located geographically, and it is probable that the radial distribution of the others from this subspecies has been accompanied by activities in evolutionary development.

The primitive type.—In tracing the phylogeny of a series of forms, it is often helpful first to determine the characters of the most primitive type. According to the foregoing principles, the requirements of such a type from which the various subspecies of *Hemizonia congesta* may have descended are:

1. A paniculate inflorescence.
2. Yellow ray-flowers.
3. An abundantly glandular pubescence.
4. A geographic distribution such as to permit of a contact, past or present, with its derivatives.
5. The absence of highly specialized features, such as elongated tips to the involucral bracts, modified upper leaves, unusual pubescence, etc.

The only form fulfilling all of these requirements is *lutescens*, a subspecies of rather restricted range in Marin County, California, and the district immediately northward. The genetic evidence also favors the conception that *lutescens* is the most primitive subspecies. It has in garden cultures proved to be capable of producing types resembling *luzulaefolia* in size and habit of plant (pl. 7), while a few *lutescens* plants, of known pedigree, have borne white or practically white flowers. Furthermore, it was found that artificial hybrids can be

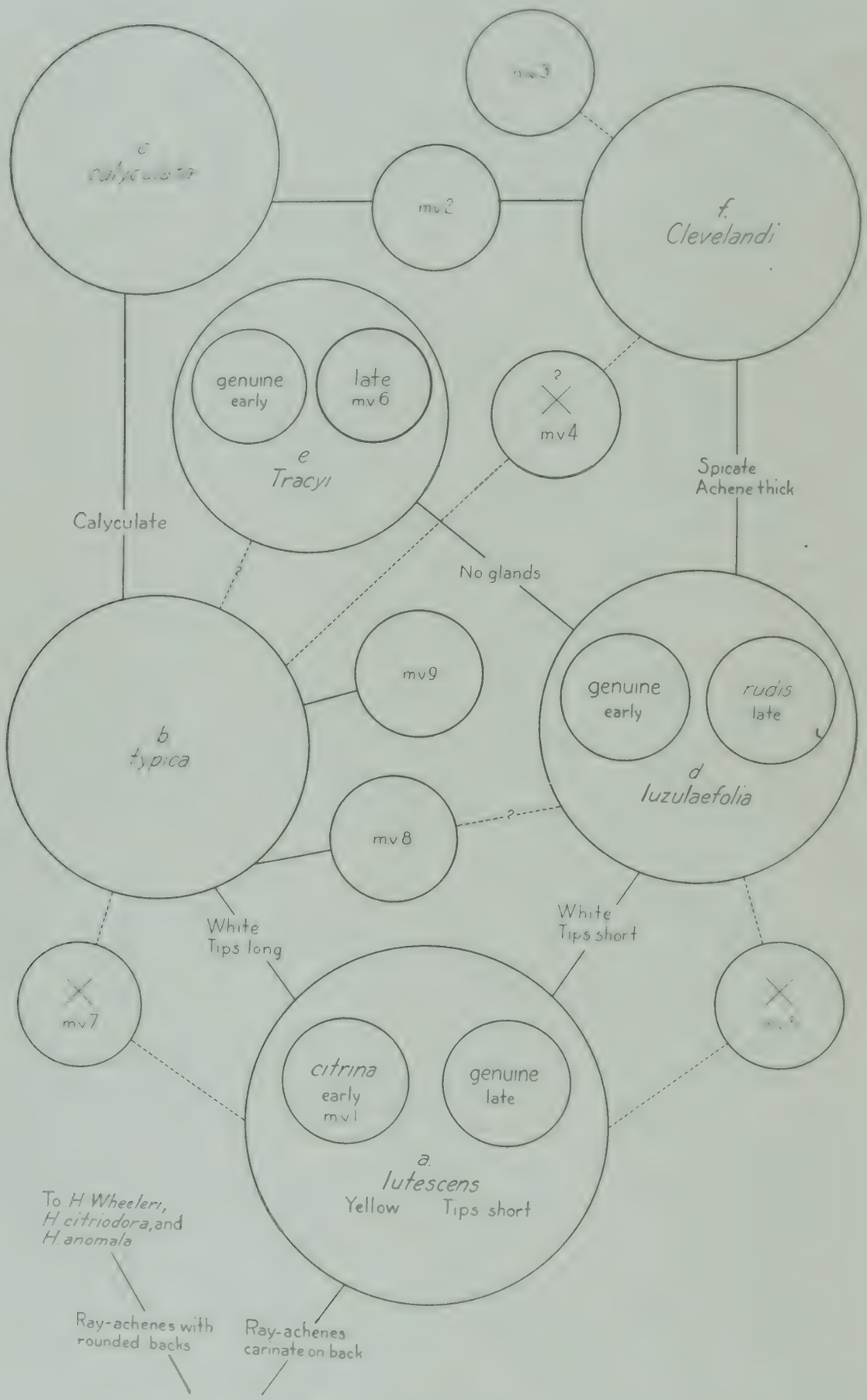
c
Calyculate ?
mv 3
mv 2
f.
Clevelandi
genuine
early
late
mv 6
e
Tracyi
?
mv 4
Spicate
Achene thick
Calyculate
No glands
mv 9
genuine
early
rudis
late
d
luzulaefolia
b
typica
mv 8
White
Tips long
White
Tips short
mv 7
citrina
early
mv 1
genuine
late
a.
lutescens
Yellow Tips short
To H. Wheeleri,
H. citriodora, and
H. anomala
Ray-achenes with
rounded backs
Ray-achenes
carinate on back

Fig. 1 (see p. 33)

easily made by crossing *lutescens* with *typica, lutescens* with *luzulaefolia,* and *typica* with *luzulaefolia.* Crosses involving the other subspecies have not been attempted. In each case the F_1 hybrids are highly fertile and intermediate in character, although in hybrids having *typica* for one parent certain *typica* characters were dominant (pl. 3, figs. 3, 4).

Sketch of the evolution of the subspecies.—With *lutescens* placed at the beginning of the phylogenetic series, as seems logical from the evidence just presented, it is found that the remaining subspecies can be arranged along two branches which diverge from this comparatively primitive stock. These are indicated on the accompanying chart and for convenience may be referred to as the *typica* and the *luzulaefolia* branches.

It is unfortunate that the first form to receive taxonomic recognition was the one here called *typica* instead of the phylogenetic type, later named as *lutescens;* but early botanists were obliged to name species in the order in which they came to light and later workers are bound by codes of convenience to follow their usage. At any rate, this subspecies *typica* is almost certainly a derivative of *lutescens,* from which it is not even yet wholly separated. It has suffered (or profited?) from the loss of yellow pigment in its ray-flowers and the pubescence has become less glandular and more shaggy. It has also shortened the peduncles, thus making the heads more or less congested. The most notable development, however, has been in the elongation of the flat tips to the bracts of the involucre. In the taxonomic sense there is complete intergradation in all of these characters and obvious hybrids are abundant where the ranges meet, as in eastern Marin County. That these intermediate forms actually are hybrids is all but proved by the production of closely similar forms through crossing in the garden experiments. It is because of this close connection through intermediate forms and the presence of hybrids that this line is assumed to have sprung directly from *lutescens* rather than from *luzulaefolia.*

Fig. 1. Chart of relationships of the subspecies and minor variations of *Hemizona congesta.* The 6 largest circles represent the 6 subspecies; 3 of these have definite early and late variations indicated by the smaller, included circles; other minor variations are placed outside the main circles in order to express either a connection between the subspecies or a divergence in characters. The numbered minor variations (abbreviated to m.v.) and natural hybrids are described in the text. Numerous additional variations known in nature and artificial hybrids and strains are not shown on the chart. Because of these intermediates, it would be better if all of the circles could have been shown as merging along their borders.

This latter subspecies seems also to have come from *lutescens*, and by but a single character difference, namely, the loss of yellow pigment in the ray-flowers. Of course, each subspecies includes numerous biotypes differing from one another in other features—branching, leafiness, relative abundance of glandular or of silky hairs, size of heads, etc.—so that some forms of one are exceedingly unlike certain forms of the others, but these are believed to be minor variations within each of the subspecies. Color is taken as of more importance, for after assembling all of the variations into two groups based upon color, it is found that these occupy rather well-defined geographic areas. *H. c. luzulaefolia* is by far the most abundant and widespread of all the subspecies. Around the head of San Francisco Bay it meets the range of *lutescens*, with which it freely hybridizes (see minor variation 5). From here it ranges north to the upper Sacramento Valley and south in the Coast Range valleys as far as San Luis Obispo.

Along the northwestern borders of its range *luzulaefolia* passes over into *Tracyi*, while to the north and northeast it yields to *Clevelandi*. The former has undergone a notable reduction in the number and size of its glands, so that the entire herbage has a smooth appearance and lacks the "ill odor and vile stickiness" of *luzulaefolia*. A tendency toward elongation of the bract-tips (as brought out in table 1), suggests a possible origin by hybridization between *typica* and *luzulaefolia*, although these are not known to be in contact at the present time. However this may be, intergrading forms are much more suggestive of the latter than of the former subspecies.

As regards habit, the subspecies *Clevelandi* is perhaps the most outstanding of all of the forms. It is plainly a derivative from *luzulaefolia*, at least as to its most obvious feature, namely, the subspicate or subracemose arrangement of the heads (p. 29). This condition has been brought about by a reduction in the length of the peduncle, continuing so far in some cases that the head is sessile on the branch. A more fundamental modification is in the shape of the ray-achenes, as already discussed, but here, too, all degrees of differentiation are encountered, so that the form cannot well be set off as a distinct species.

There remains for final consideration one subspecies here described for the first time, namely, *calyculata*. This has stiff, harsh twigs with very numerous, rigid, almost brittle leaves, the upper ones surrounding the heads like an outer involucre, and the herbage is copiously

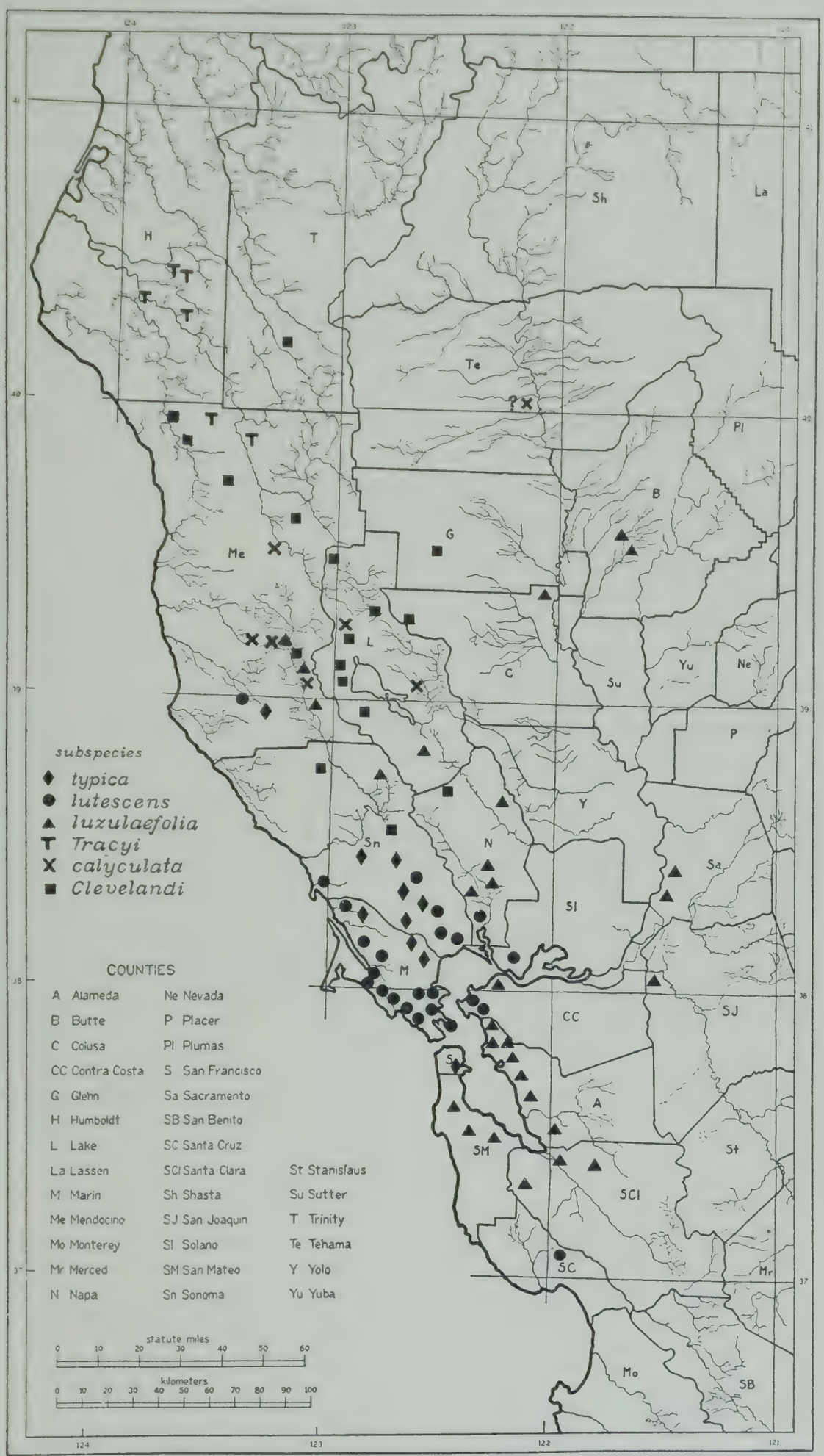

Fig. 2. Distributional map of the subspecies of *Hemizonia congesta*, in western California. Additional distribution in San Luis Obispo County, to the south, and into southern Oregon, on the north, is not shown.

glandular as well as villous. This combination of characters at once suggests a hybrid origin. The essentially sessile heads, the well-developed upper foliage, and especially the long-tipped bracts are apparently derived from *typica*, but the remarkable glands are very different from anything found in that subspecies. A derivation entirely from *typica* would necessitate the almost impossible assumption that the glandular character formerly much suppressed in the evolution of this line from *lutescens* was somehow regained in passing on to *calyculata;* in other words, that this is a case of reversion. A more reasonable assumption is that this trait came from *Clevelandi*, where also it is strongly developed. Too little is known regarding the distribution of tarweeds in the area from which *calyculata* comes, especially Lake and eastern Mendocino counties, but the ranges of the two suggested parents come very close together, if indeed they do not actually meet. Since the form under consideration produces well-formed seed, it is probably able to perpetuate itself over the limited area where it grows.

In summarizing it may be said that the subspecies *lutescens* is probably the most primitive form and occupies a small area near the center of distribution of the species. Evolution has proceeded from this in two directions, yielding two phylogenetic branches. One of these has produced *typica*, which later joined with a member of the second branch to produce *calyculata*. On the second branch is *luzulaefolia*, the most important subspecies, from which has arisen by modification *Tracyi* on the one hand and *Clevelandi* on the other. Although a speculative element enters into these conclusions, they seem to be supported by all of the available evidence.

TAXONOMIC TREATMENT

Hemizonia congesta DeCandolle

Prodr., vol. 5, 1836, p. 692.

An erect annual herb, usually 2 to 8 dm. high, simple below, corymbosely branched above, the stem somewhat villous and also more or less glandular, often very densely so and the glands then large and stalked; leaves often crowded near the base but sometimes equally distributed to midway of the stem, above which they are reduced to short bracts; lower and basal leaves lanceolate or ligulate, acute or somewhat obtuse, acutely denticulate with few teeth or entire, 4 to 18 cm. long, 2 to 10 mm. wide, with several nearly parallel nerves from the base, varying from scabro-puberulent to silvery-silky with appressed hairs, sometimes also slightly glandular; inflorescence corymbiform or paniculate in its primary branching, the heads either scattered or congested or in one subspecies spicately or racemosely arranged along the branches, sparsely to copiously villous, also viscid to coarsely and densely glandular; bracts of the inflorescence linear to lanceolate, sometimes notably broadened at the sessile base; involucre campanulate, 4 to 8 mm. high, about as broad, each bract with a deeply concave basal portion, or body, which enfolds the ray-achene and a flat lanceolate tip, ray-flowers 6 to 12, usually 8; ligules 5 to 10 mm. long, 6 to 9 mm. wide, cleft into three elliptic obtuse lobes, the middle one of which is much the narrowest, white or yellow, veined especially on the back with pink or purple, commonly glandular-puberulent on the back; disk-flowers about 20 to 60, the funnelform corollas 2.5 to 3.5 mm. long; bracts of the receptacle all more or less united, especially the outer ones, which surround the disk like a cup with a toothed border; ray-achenes fertile, obovate-triangular, with a dorsal and two lateral angles, the inner or ventral face nearly plane, the surface smooth and shining, the base abruptly narrowed to a slender inflexed stipe which is white or brownish at the insertion on the receptacle, the terminal areola slightly eccentric and near the inner edge but not prolonged into a hook or beak; disk-achenes sterile; pappus none; chromosomes (examined only in microspore mother cells of subspp. *typica*, *lutescens*, and *luzulaefolia*) 12 pairs of approximately the same size and shape.

Key to the Subspecies of Hemizonia congesta

Ligules of ray-flowers yellow, veined with reddish or purplish.....(*a*) **lutescens**
Ligules of ray-flowers white, veined with reddish or purplish.
  Flat tip of involucral bracts mostly longer than the body; entire bract 6 to 12 mm. long.
    Bracts of the inflorescence scarcely or not at all overtopping the heads, softly villous and moderately glandular (strongly glandular in minor variation 8) .....(*b*) **typica**

Bracts of the inflorescence overtopping the heads around which they form a false whorl, somewhat villous but also scabrid and notably glandular .....(*c*) **calyculata**

Flat tip of involucral bracts mostly shorter than the body; entire bract 3.5 to 7 mm. long.

Inflorescence paniculate, the heads terminating short branches; breadth of ray-achenes about 50 to 60 per cent of the length.

Herbage conspicuously glandular, especially the stems and inflorescence, strongly scented .....(*d*) **luzulaefolia**

Herbage obscurely glandular, even the inflorescence scarcely more than viscidulous, nearly inodorous .....(*e*) **Tracyi**

Inflorescence somewhat spicate, the heads disposed to be sessile along the branches as well as terminal; breadth of ray-achenes 60 to 70 per cent of the length .....(*f*) **Clevelandi**

[Abbreviations used in designating herbaria under citation of specimens:

DS Dudley Herbarium of Stanford University,
Gr Gray Herbarium of Harvard University,
SF Herbarium of California Academy of Sciences,
UC Herbarium of University of California including Brandegee Herbarium,
US United States National Herbarium.]

a. H. congesta lutescens (Greene) new comb.

H. luzulaefolia var. *lutescens* Greene, Bull. Torr. Club, vol. 9, 1882, p. 16.
H. citrina Greene, Man. Bay Reg. Bot. 1894, p. 194. (The early flowering form. See minor variation 1.)
H. luzulaefolia var. *citrina* Jepson, Fl. W. Mid. Calif. ed. 1, 1901, p. 530.

Herbage villous and glandular, the long non-glandular hairs of the lower leaves more or less matted, sometimes so long and closely appressed as to silver the entire surface, the shorter more spreading and gland-tipped hairs increasingly abundant up the stem and in the inflorescence which is thus moderately viscid and strong-scented; lower leaves crowded, linear-lanceolate to broadly lanceolate, acuminate, closely or remotely denticulate to entire, 5 to 15 cm. long, 4 to 10 mm. wide, with 2 or 4 nerves paralleling the midrib, or these obscure in very narrow leaves; middle cauline leaves numerous and similar to the basal in early flowering forms (minor variation 1), less numerous and much reduced in size in the typical autumnal form; inflorescence paniculate, often widely so, most of the heads pedunculed; bracts of the inflorescence linear or lanceolate, sessile by a sometimes broad base, the upper ones reduced and the heads therefore naked; bracts of the involucre 4.5 to 6.5 mm. long, the flat tip shorter than or rarely equaling the body; ligules yellow (the types described as rich cream yellow to lemon yellow but these doubtless with some *luzulaefolia* influence), veined with pink or purple; breadth of ray-achenes 40 to 60 or rarely 63 per cent of the length.

Only near the coast, northern Monterey County, Marin County, and the northeast shores of San Francisco Bay to Napa and Mendocino counties, all in California. Types collected in the vicinity of San Pablo and at Vallejo by Greene.

South side of San Juan Grade, Monterey County, July 22, 1915, *Hall 10061* (UC, ligules light yellow, perhaps a hybrid with *luzulaefolia*)[b]; Rodeo Lagoon, July 11, 1905, *Brandegee* (UC)[a]; Bolinas Bay, south of Willow Camp, June 7, 1921, *Hall 11272* (UC)[c]; north of Bolinas, October 2, 1914, *Hall 9890b* (UC)[a]; Ross Valley, November, 1893, *Jepson* (UC)[a]; Mount Tamalpais, June 14, 1892, *Brandegee* (UC)[a]; between Mount Tamalpais and Fairfax, October 26, 1915, *Abrams 5612* (DS)[a]; Marin County, April, 1886, *Greene* (UC)[c]; Olema, June 7, 1886, *Brandegee* (UC)[c]; Tomales Bay, April 16, 1886, *Greene* (UC, probably the type of *citrina*, minor variation 1)[d]; Novato, July 24, 1916, *Hall 10252* (UC)[a]; San Rafael to Petaluma, September 18, 1897, *Davy* (UC)[a]; 12 km. northwest of Petaluma, July 23, 1916, *Hall 10243* (UC)[a]; 22 km. northwest of Petaluma, July 23, 1916, *Hall 10246b* (UC)[c]; south slopes of Tiburon Peninsula, May 31, 1909, *Walker 185* (UC, DS)[c]; same locality, June 13, 1915, *Babcock c, d, e, f* (UC)[c]; type collection, San Pablo, September, 1881, *Greene* (Gr)[a]; near San Pablo, Contra Costa County, August 23 and September 13, 1914, *Hall 9860, 9861, 9875* (UC)[a]; Giant, Contra Costa County, July 20, 1916, *Hall* (UC)[a]; Vallejo, *Elmer 4945* (Gr); near Napa Junction and at Collins, Napa County, August 12, 1915, *Hall 10094, 10095, 10096, 10097* (UC)[a]; Suisun to Benicia, Solano County, September 24, 1917, *Abrams 6856* (DS)[a]; near Sebastopol, *Heller 6054* (Gr, NY, Phila, DS)[c]; near Tocaloma, July 22, 1916, *Hall 10238* (UC)[a]; Bodega Bay, July 23, 1916, *Hall 10248* (UC)[b]; south of Booneville, Mendocino County, July 10, 1909, *McMurphy 509* (DS)[c].

[a] The genuine form of *lutescens*, late flowering, the leaves chiefly basal and at least some of them silvery-silky.

[b] Same form as *a* but none of the leaves silvery-silky.

[c] An early flowering form with long leaves well up the stem, at least some of the lower ones silvery-silky.

[d] The same form as *c* but none of the leaves silvery-silky. This is *citrina*, that is, minor variation 1. The variation in the degree of silkiness and leafiness renders the placing of some of the specimens as to form exceedingly doubtful. See further on page 30.

The relationships of this subspecies are discussed in connection with others which are supposed to have evolved from it, particularly *typica* and *luzulaefolia*. Its most notable modification is described as minor variation 1 (p. 51).

b. H. congesta typica

H. congesta DC., Prodr., vol. 5, 1836, p. 692.

Herbage densely villous throughout, the hairs sometimes appressed on the lower leaves but never so closely as to render them silky, also slightly viscid toward the heads but only sparsely and very minutely if at all glandular; lower leaves ligulate, acute, denticulate with low and remote teeth or entire, 6 to 12 cm. long, 4 to 8 mm. wide, with 2 faint nerves paralleling the strong midrib; middle cauline leaves similar to the basal but moderately reduced in number and size; inflorescence corymbiform or paniculate, the heads terminating short branches and either in congested clusters of 2 or 3 each or solitary, often also a few lateral heads along the branches but these commonly fail to develop, or in reduced plants the heads all subspicate along the simple stem, or even solitary and terminal; bracts of the inflorescence lanceolate from a broad sessile base, regularly reduced upward, none overtopping the heads; bracts of the involucre 6 to 9 mm. long, the flat tip from nearly equaling to much longer than the body; ligules white (varying to cream color or lemon yellow when growing near *lutescens*), veined with pink or purplish; breadth of ray-achenes usually 50 to 60 per cent of the length.

California from San Francisco Peninsula north to Mendocino County and probably to the borders of Humboldt County; most abundant in eastern Marin and eastern Sonoma counties; perhaps never in the immediate vicinity of the ocean. Type locality, "California."

Type collection, *Douglas* (Gr, a piece from the DeCandolle herbarium, transmitted by Bentham, here also a fragment ex-herb. Hooker, also a specimen ex-hort. Cantab., the original seed doubtless of the Douglas collection); summit of ridge between Colma and San Bruno, south of San Francisco, June 13, 1909, *McMurphy* (DS); southern part of San Francisco, *Brandegee* (UC); 10 km. north of San Rafael, Marin County, *Hall 10236* (UC); Tomales, Marin County, June, 1886, *Brandegee* (UC); 6 to 10 km. west of Petaluma, Sonoma County, *Hall 10240, 10241, 10241b* (UC); near Sonoma, *McMurphy 708* (DS); Verano, Sonoma County, 1888, *Brandegee* (UC); Santa Rosa, Sonoma County, *Heller 5637* (UC, DS, a reduced form described as minor variation 9); between Santa Rosa and Sebastopol, June, 1905, *Brandegee* (UC); near Fulton, Sonoma County, September 27, 1908, *McMurphy* (DS); Pudding Creek, Mendocino County, June 25, 1894, *Eastwood* (UC).

In its extreme form, as exemplified by the types, this subspecies is easily distinguished from the others by its copious, shaggy, pubescence, almost entire absence of glands, long involucral bracts, and characteristic grouping of the heads into close terminal clusters. There is a grading off in all of these characters, however, and the form is so closely interwoven with the other subspecies, by hybridization or by gradual variation or by both, that its specific separation is by no means complete. It is in contact with *lutescens* throughout most of its range and hybridizes freely with it. These hybrids exhibit all degrees of yellowing of the ligules and act in this respect like the artificial hybrids between *luzulaefolia* and *lutescens* (see p. 56). Variations in pubescence may also be the effect of crossing, but, as already shown, this feature is extremely variable within each of the subspecies and the differences are only quantitative. An exceptionally perplexing instance is that of minor variation 8 in which a heavily glandular pubescence, similar to that of *luzulaefolia*, occurs on plants which by all other criteria would be classed as typical *congesta*, and this form, moreover, inhabits a limited geographic area to the exclusion of all other forms. Variation in the arrangement of the heads on single plants, apparently not of hybrid origin, is illustrated in many herbarium specimens, where it may also be noted that inflorescences in *typica* and *luzulaefolia* are sometimes almost identical.

Perhaps the best differentiating feature for the recognition of *typica* is found in the elongated involucral bracts, the flat tips of which are usually longer than the body. This feature recurs in *calyculata* but here it is associated with others, so that there need be no confusion between these two subspecies. More troublesome is the too frequent occurrence of bracts in which the tips only equal or in some cases actually are shorter than the body. The extent of this fluctuation is brought out in table 1.

In the light of the foregoing evidence it seems impossible to retain *congesta* as a species distinct from the other subspecies here brought into it unless one is willing to lower the species standard to such an extent as to admit as species two forms occupying the same area and having intermediate variations which can be placed as neither the one nor the other.

c. **H. congesta calyculata** n. subsp.

Plate 1

Herbage moderately villous and densely glandular, the villous hairs long, white, and somewhat appressed on lower part of stem and on lower petioles, the glandular hairs increasingly abundant up the stem, the inflorescence densely dotted with dark glands each terminating a short stiff trichome; lower leaves only moderately crowded, narrowly lanceolate, rather obtuse, remotely and acutely denticulate, 4 to 8 cm. long, 2 to 5 mm. wide, strongly ribbed and with 2 additional parallel nerves; middle cauline leaves similar to the basal ones but more scattered, moderately reduced in size; inflorescence corymbiform-paniculate, the heads terminating rigid leafy-bracted branches which sometimes also bear undeveloped heads in the leaf-axils and thus resemble immature spikes; bracts of the inflorescence linear-lanceolate, sessile, only slightly broadened at base, the uppermost ones about 10 mm. long, crowded around and exceeding the heads; bracts of the involucre 6 to 12 mm. long, the flat tip exceeding the body; ligules white, veined with purple on the back; breadth of ray-achenes 55 to 60 per cent of the length.

Northern Lake and eastern Mendocino counties, California; an aberrant form from the Sacramento Valley. Type specimen from clay slopes 5 km. east of Orr's Springs, Mendocino County, California, August 13, 1924, *Hall 12094* (UC). Other specimens which agree closely with the above description, except that the spicate tendency is often more obvious and the involucral bracts are sometimes much shorter, are:

Sulphur Bank, Lake County, October, 1900, *Bowman* (UC); hills near Orr's Springs, Mendocino County, July 25, 1903, and July 20, 1909, *McMurphy* (DS); Willits, Mendocino County, June 17, *Brandegee* (UC); south side of Elk Mountain, Lake County, July 27, 1913, *Hall 9588* (UC). A specimen from Red Bluff (September 20, 1892, *Brandegee*) and doubtfully referred here is discussed below.

The characterization given above will serve to distinguish this from the other subspecies of *Hemizonia congesta*. The plants are often quite small, many measuring only 1.5 to 3 dm. high, but in the type collection some are as much as 6 dm. in height. The long bracts of the inflorescence persist around the naked receptacle after the flowers and involucre have fallen away and simulate an outer involucre or calyx, as suggested in the proposed name. The receptacle is bracteate throughout, with the outer circle of bracts firmly united into a cup with an acutely toothed border.

The long involucral bracts, and especially their long tips, immediately suggest a connection with *typica,* but the other features are more like those of *Clevelandi.* The pubescence of the lower leaves and stem is much the same as in the latter and the large stalked glands of the inflorescence are almost the same, although more abundant. There is also an approach to *Clevelandi* in the tendency toward a spicate type of inflorescence and in the rather broad achenes. It seems, therefore, that *calyculata* may have arisen by hybridization between the two subspecies mentioned, but that it is now self-perpetuating. Both of the supposed parents occur near the eastern borders of its area of distribution, but at other places *typica* is missing. A single collection comes from very much farther east, namely from Red Bluff, in the Sacramento Valley, at least 130 km. (80 miles) from the nearest plants of *typica,* but not far from *Clevelandi* (see minor variation 2, p. 52). The plants here collected show a strong influence of the latter in the very broad achenes, 6 of which give ratios of breadth to length of 70, 70, 74, 75, 77, and 79 per cent, respectively. A derivation from *Clevelandi* alone is strongly suggested, at least for this more easterly, broad-achened form. On this assumption, however, the long involucral bracts would constitute a variation parallel to that developed during the separation of *typica* from *lutescens.* It is to avoid this unsubstantiated assumption that the theory of a hybrid origin is favored.

The differentiating characters of this form were independently noted by J. I. W. McMurphy, who at one time labeled specimens of it in the Dudley Herbarium as belonging to an undescribed species related to *H. congesta* and *H. Clevelandi.* It is with Professor McMurphy's permission that the form is now described as a subspecies, although he is still of the opinion that it is worthy of specific rank.

d. **H. congesta luzulaefolia** (DC.)

H. luzulaefolia DC., Prodr., vol. 5, 1836, p. 692.
H. sericea H. and A. Bot. Beech., 1840, p. 356(?).
H. rudis Benth. Bot. Sulph., 1844, p. 31. (The late flowering form. See minor variation 10.)
H. luzulaefolia var. *fragarioides* Kell. Hesperian, vol 5, 1860, p. 394, with fig. on p. 395; Proc. Calif. Acad. Sci., vol. 2, 1860, p. 69, fig. 14.
H. grandiflora Abrams, Torreya, vol. 2, 1902, p. 122. (The early flowering form. See further under minor variation 10.)

Herbage villous and glandular, the long non-glandular hairs of the lower leaves more or less appressed, sometimes so much so as to silver the entire surface, the shorter and gland-tipped hairs very abundant along the stem and in the inflorescence which is thus rendered exceed-

ingly viscid and strong-scented; lower leaves crowded, linear-lanceolate, acuminate, remotely and often minutely dentate or entire, 8 to 18 cm. long, 4 to 10 mm. wide, with 2 to 6 faint nerves paralleling the midrib; middle cauline leaves similar to the basal in early flowering forms (although seldom silvery-pubescent), much reduced in autumnal forms (see minor variation 10); inflorescence widely paniculate, most of the heads pedunculed; bracts of the inflorescence lanceolate, sessile, the upper ones much reduced and the heads therefore naked; bracts of the involucre 3.3 to 6 or rarely 6.5 mm. long, the flat tip always shorter than the body; ligules white, veined with pink or purple; breadth of ray-achenes 50 to 60 per cent of the length.

Coast counties of California from San Luis Obispo to San Francisco Bay, thence north from the east shores of the bay to eastern Mendocino County and east to Stockton and Butte County; most abundant in the middle portion of its range; scarce in the northern part, where largely replaced by *Clevelandi*. Type locality, "California."

Type collection, *Douglas* (Gr); Morro, coast of San Luis Obispo County, *Barber* (UC); San Luis Obispo, August 24, 1909, *Abrams* (DS)[a]; Smith Creek, Mount Hamilton Road, October 3, 1908, *McMurphy* (DS)[a]; foothills west of Los Gatos, September 12, 1904, *Heller 7536* (UC, DS)[a]; near Newark, east side San Francisco Bay, October 17, 1908, *McMurphy* (DS)[a]; Santa Clara, September 19, 1908, *McMurphy* (DS)[a]; Saratoga, Santa Clara County, September, 1893, *Davy 320* (UC)[a]; Stanford University, September 14, 1901, *Baker 49* (UC)[a]; Crystal Springs, San Mateo County, May 11, 1902, *Abrams 2446* (DS, type collection of *H. grandiflora*, see under minor variation 10); same locality, June 30, 1903, *Baker 3350* (UC); hills west of Millbrae, San Mateo County, June 13, 1909, *McMurphy* (DS); Belmont, San Mateo County, June 17, 1893, *Davy 784* (UC); near Hayward, Alameda County, September 24, 1909, *McMurphy* (DS)[a]; Walnut Creek, Contra Costa County, September 25, 1909, *McMurphy* (DS)[a]; Berkeley, June, 1891, *Bioletti* (UC); Berkeley, July 28, 1909, *Walker 1722* (UC, DS, a form intermediate to *H. rudis*, minor variation 10); Richmond, Contra Costa County, August 23, 1914, and July 24, 1916, *Hall 9858, 10253, 10254* (UC)[a]; San Pablo, Contra Costa County, August 23 and September 19, 1914, *Hall 9860, 9883* (UC)[a]; between Benicia and Cordelia, Solano County, May 9, 1917, *Hall 10287* (UC); 13 km. west of Petaluma, July 23, 1916, *Hall* (UC)[a]; Collins, Napa County, August 12, 1915, *Hall 10097* (UC)[a]; 7 km. south of Napa, August 6, 1916, *Hall 10261, 10262* (UC)[a]; Suisun,

September 22, 1907, *Walker 1006* (UC)[a]; Laguna Valley, Solano County, September 28, 1893, *Jepson* (UC)[a]; Kenwood, Sonoma County, August 8, 1909, *McMurphy 705* (DS)[a]; Chauvert's, Sonoma County, July, 1892, *Bioletti* (UC); near the geysers, Sonoma County, May 29, 1909, *McMurphy* (DS); Ukiah Valley, Mendocino County, July 13, 1913, *Hall 9454* (UC, only slightly glandular but otherwise typical of the autumn form)[a]; Aetna Springs, Napa County, August 23, 1882, *Cleveland* (UC)[a]; near Middletown, Lake County, August 16, 1911, *Brandegee* (UC)[a]; near Stockton, October 2, 1907, *Brandegee* (UC)[a]; near Elk Grove Park, Sacramento County, September, 1917, *Abrams 6752* (DS)[a]; between Sacramento and Galt, August 3, 1914, *Hall 9839* (UC)[a]; near Williams, Colusa County, "common south to Vacaville," August 16, 1916, *Hall* (UC)[a]; Princeton, Colusa County, September 14, 1905, *Chandler* (UC)[a]; 13 km. north of Oroville, October 7, 1913, *Heller 11147* (UC, DS)[a]; near Chico, Butte County, August 1, 1914, *Hall 9825* (UC)[a]; near Durham, Butte County, September 9, 1916, *Heller 12653* (SF, DS)[a].

[a] The form commonly maturing in late summer and autumn; stem leaves much reduced, except those in the basal rosette; heads for the most part smaller than in the spring form. See further under *H. rudis*, minor variation 10 (p. 54).

This is by far the most abundant and widespread subspecies and the one which, because of usage, it would be the most desirable to retain in specific rank. Although there is some evidence of direct hybridization with typical *congesta* and the consequent production of intermediate forms, the phylogenetic connection is most marked through *lutescens*. The impossibility of maintaining the latter as specifically distinct from *congesta* has been brought out in discussing the relationships of *congesta typica*. It now remains to demonstrate the close connection between *luzulaefolia* and *lutescens*. This is easily done since they differ in only one character, namely, the color of the ligules. In all other features the variations of the one are exactly paralleled by the variations of the other. Both have a spring form with large leaves carried well up the stem, and large heads, and both have a more glandular autumn form with leaves mostly basal and smaller heads (minor variations 1 and 10, pp. 52, 54); in both subspecies are to be found forms in which most of the leaves are silvery-silky, and other forms in which they are scarcely, if at all, silky; and in both the extent of variation in features of the involucral bracts and of achenes is about the same (table 1).

The criterion of color, taken alone, is one which perhaps no taxonomist would advance as of specific merit. As will be shown farther on (p. 78), changes in color are here probably due to a single pair of genetic factors but certain other pairs of genes have a modifying effect on the degree of yellow color.

As regards geographic distribution, it is to be noted that *luzulaefolia* occupies an area different from that of *lutescens*, and this constitutes the best claim of the latter to subspecific rank. The ranges are in contact, however, for nearly the whole front of the area occupied by *lutescens* (fig. 2), and along this line the two freely interbreed, with a resulting intergradation in color that is complete, at least so far as can be determined by observation. That these intermediates, more fully discussed under minor variation 5, are hybrids is attested by the production of their exact counterparts through artificial hybridization (p. 56).

The conclusion thus seems inescapable that *luzulaefolia* is very intimately connected with *lutescens* and through this with typical *congesta*.

e. H. congesta Tracyi n. subsp.

Plate 2

Herbage minutely crisp-puberulent throughout, also slightly villous on the lower leaves and in the inflorescence, slightly viscid on peduncles and involucres but scarcely at all glandular;[3] lower leaves not crowded, lanceolate, somewhat obtuse, entire or remotely denticulate, 8 to 12 cm. long, 4 to 6 mm. wide, with 2 rather prominent nerves paralleling the midrib; middle cauline leaves similar, rather equally distributed, only slightly reduced (only the lower leaves elongated in minor variation 6, p. 53); inflorescence openly corymbiform, the heads terminating divergent peduncles, these mostly 2 to 8 cm. long; bracts of the inflorescence lanceolate from an ovate sessile base, the lower about 10 mm. long, the upper ones smaller and the heads therefore naked; bracts of the involucre 6 to 7 mm. long, the flat tip usually a little shorter than the body; ligules white, probably veined with pink or purple; breadth of ray-achenes 50 to 63 per cent of their length.

Humboldt County, California, said to be very abundant in the hill district of the eastern part of the county, where it grows to the exclusion of other subspecies; also in adjacent Mendocino County. Type specimen, Valley of Van Duzen River opposite Buck Mountain, Humboldt County, California, altitude 760 meters, June 27 to July

[3] The foregoing description is drawn from the type specimen. The others cited vary as follows: hairs of the inflorescence sometimes obviously but minutely gland-tipped; peduncles only 1 to 5 cm. long or some of the heads nearly sessile but never congested; bracts of the involucre 5 to 7 mm. long.

30, 1908, *Joseph P. Tracy 2754* (UC). Other specimens referrable here, all from Humboldt County, except the first two, are:

Cedar opening, Red Mountain, northern Mendocino County, July 30, 1909, *McMurphy 621* (DS)[a]; open grassy hills near Handley's, Mendocino County, July 20, 1909, *McMurphy 530* (DS)[a]; above Blue Rock, Mendocino County, July 28, 1909, *McMurphy 584* (DS)[a]; Mount Pierce, July 20, 1919, *Tracy 5183* (UC); Kneeland Prairie, June 8, 1908 and August 1, 1920, *Tracy 2629, 5348* (UC); "High Prairie" on Bald Mountain, July 5, 1914, *Tracy 4570* (UC); Yager Creek Bar, near Hydesville, "probably a waif," July 4, 1906, *Tracy 2530* (UC); Redwood Creek, May 28, 1901, *Chandler 1245* (UC); Laribee Creek, at Bosworth's, June 19, 1916, *Tracy 4708* (UC); mouth of Grizzly Creek, on Van Duzen River, July 11, 1916, *Abrams 6030* (DS).

[a] A form with leaves chiefly basal. See minor variation 6, p. 53.

In aspect this subspecies is strikingly different from that of the others. This is due chiefly to the notable reduction in both the villous and glandular types of pubescence. The herbage has a smooth, greenish or reddish appearance and is remarkably free from dust and other foreign material commonly held by the glands in some of the other subspecies. The glands are never entirely wanting but they are sometimes so sparse and minute as to require a lens for their detection. Such plants would be described as obscurely viscid rather than glandular. There are various degrees from this stage to heavily glandular. Two specimens cited above as *Tracyi* are quite glandular and therefore intermediate to *luzulaefolia* (*Tracy 5183, 5348*). In garden experiments conducted at Berkeley, which is within the area of *luzulaefolia*, it was found that although the habital characters and leafiness of *Tracyi* were maintained for several generations, there was a marked increase in the number and size of the glands, even in the first season (seeds from *Tracy 4708* grown under garden No. 8/17; specimens preserved in herb. Univ. Calif.). There is also some indication that the glandulosity increases as the season advances, and this may account in part for the change noted in garden plants.

Joseph P. Tracy, of Eureka, California, to whom we are much indebted for a splendid series of herbarium specimens of this form as well as for copious field notes and for first pointing out its distinguishing features, writes of it as follows:

It is widely different in the field from *luzulaefolia*. We have no *luzulaefolia* to the northward of the Alder Point district. The undescribed form, which I have been provisionally calling *congesta*, is one of the most abundant plants on grassy hillsides from Blocksburg northwestward to Bridgeville and Kneeland. I

passed through thousands of acres of it in full bloom on the Alder Point trip. The flowers are always white. It is not at all viscid to the touch, even around the inflorescence. It is a "winter annual," flowering in June and drying up as the hills turn yellow, which is usually the end of June here. It does not appear after the other things dry up, as does *luzulaefolia*.

The relationships are with *luzulaefolia*, of which this seems to be a northwestern derivative. The connection may be traced by comparing the more glandular specimens mentioned above with the spring form of *luzulaefolia* as represented by specimens from Crystal Springs Lake, San Mateo County (*Hall 10255*). Traces are also apparent of the influence of typical *congesta*, especially in the broad-based bracts of the inflorescence and in the rather long involucral bracts. The tips of these bracts, however, are almost always shorter than the body, and since there is no indication of the soft pubescence of *congesta typica*, nor of its congested inflorescence, the connection is perhaps remote.

f. **H. congesta Clevelandi** (Greene) n. comb.

H. Clevelandi Greene, Bull. Torr. Club, vol. 9, 1882, p. 109.

Herbage moderately villous throughout and also glandular, copiously glandular especially in the inflorescence in the typical form, less glandular and more villous in some plants (minor variation 3), the longer hairs sometimes more or less appressed but so far as known the foliage never silvery-silky; lower leaves usually not crowded, linear or linear-lanceolate, obtuse or only moderately acute, entire or remotely denticulate, 8 to 15 cm. long, 2 to 8 mm. wide, with 2 to 4 nerves paralleling the midrib or these wanting; middle cauline leaves sometimes as large as the lower and numerous, but often reduced and scattered, especially in the autumnal form; inflorescence spicate-paniculate or racemose-paniculate, that is the heads sessile or short-peduncled along the branches of an open panicle; bracts of the inflorescence linear-lanceolate, sessile, the base not especially enlarged, the upper ones scattered, not overtopping the heads; bracts of the involucre 4 to 7 mm. long, the flat tip usually shorter than the body but sometimes moderately exceeding it; ligules white, veined with purplish; breadth of ray-achenes usually 60 to 70 per cent of their length.

Warm and dry interior districts, from Sonoma and eastern Mendocino counties, California, to the Sierra foothills of Butte County and north to southern Oregon. Type locality, Allen Springs, Lake County, California (other collections from Lake and Napa counties are mentioned with the original description, which, however, was apparently based chiefly upon the material from Allen Springs).

In the following list all localities are in California except the last three. Near Healdsburg, Sonoma County, October, 1896, *King* (UC); east of Fulton, Sonoma County, September 26, 1908, *McMurphy* (DS); Calistoga, Napa County, August, 1883, *Greene* (UC); Vichy Springs near Ukiah, Mendocino County, *McMurphy 536* (DS); Willits, Mendocino County, July 22, 1908, and July 6, 1910, *McMurphy* (DS); Comptche, Mendocino County, June 18, 1910, *McMurphy* (DS); Laytonville, Mendocino County, *Eastwood 9337* (SF); type collection, 1881, *Cleveland* (Gr, UC); Bradford's, Lake County, August 22, 1883, *Greene* (UC); near Lakeport, *Hall 11932, 11935* (UC); Elk Mountain, northern Lake County, *Tracy 2319* (UC)[a]; Mount Sandhedrin, northern Lake County, *Hall 9502* (UC)[a]; Burnt Ranch, Trinity County, *Tracy 5217* (UC)[a]; hills west of Leesville, Colusa County, *Heller 12358* (UC, SF, DS)[a]; mud flat on the Newville-Covello road, Glenn County, *Heller 11530* (UC, SF, DS)[a]; Big Butte Creek, Josephine County, Oregon, *Heller 12965* (SF, UC, DS); Deer Creek, Oregon, *Howell* (UC, US); Bear Creek, Jackson County, Oregon, *Cusick 2901* (UC, DS, US in part).

[a] Less glandular and more villous than in typical *Clevelandi.* See further under minor variation 3.

The direct derivation of this subspecies from *luzulaefolia* is almost established. The separation is not yet complete and the intermediate stages can therefore be traced with some degree of certainty. The differences lie in two features only, namely, the tendencies toward a spicate inflorescence and toward shorter and relatively broader achenes in *Clevelandi.* The natural derivation of the so-called spikes from panicles and the reversal of this process in garden cultures has already been mentioned (p. 29). In nearly all collections some of the heads are borne on peduncles of varying lengths and in many cases it is doubtful whether the inflorescence should be classed as spicate or paniculate. As examples of *Clevelandi,* but with some of the heads paniculately scattered, may be cited collections from southern Oregon (*Heller 12965*), and from Lake County, California (*Tracy 2319; Hall 9502*). Even more troublesome is a sheet at the United States National Herbarium of plants from Oregon (*Cusick 2901,* on sheet 528661). The middle specimen is definitely spicate, but to the left of it is one in which the heads are terminal on ascending branches 4 to 6 cm. long. In all other respects the two plants are closely similar. (The right hand specimen is *Calycadenia ciliosa,* mixed with the others by mistake, probably in collecting.)

In connection with the original description, attention was called to the manner in which the involucral bracts hold the achenes. It was there stated that, whereas in *luzulaefolia* the margins are folded over the inner face of the achene, so that the seeds falling to the ground carry the scales with them, in *Clevelandi* the achenes "are in this respect wholly free, and falling, leave the scales still adhering to the receptacle." But field observations do not bear out these statements, for *luzulaefolia* often drops its achenes while still holding the bracts, and conversely, *Clevelandi* often drops the bract and seed together. Both seeds and scales shatter off so easily when fully mature that any tendency in one direction or the other would be difficult of demonstration. Moreover, an examination of herbarium specimens fails to disclose any marked difference in the extent to which the achenes are covered by the margins of the bracts. If such difference exists, it is doubtless associated with a difference in the shape of the achenes. It is found by actual measurement and tabulation that the achenes of *Clevelandi* average broader in proportion to their length than the achenes of any other of the subspecies (table 1). Theoretically this should bulge the bract outward in the middle and thus permit the seed to escape more readily.

The breadth to length ratio of the achenes is, of course, only an expression of shape and since it requires some patience in measurement and computation it will never be a popular criterion for the identification of specimens. But when considered as the expression of a tendency it is very useful as indicating a phylogenetic deviation that might otherwise escape detection. This achenial character and the tendency toward a spicate inflorescence, as mentioned above, constitute the only criteria for the separation of *Clevelandi* and *luzulaefolia*. Whether or not the differences are sufficiently important and well defined to justify the retention of both of these in specific rank will depend largely upon one's conception of what a species should be.

MINOR VARIATIONS AND NATURAL HYBRIDS

The following enumeration includes only the more outstanding forms, especially those which have previously received taxonomic recognition. There are, in addition, numerous natural ecads. That some of these are seasonal is suggested by the fact that individuals which get an early start are usually more leafy than those which produce most of their growth during the dry summer and autumn, and that the individual leaves are broader in spring forms. There is a gradual shading off in these characters as the season advances, except in plants growing in depressions or other situations where kept moist. Garden

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conditions also result in the production of plants more robust and leafy than the wild parents from which the seed was taken. The condition of the soil has much to do with stature and branching and therefore with the appearance of the inflorescence. Thus it has been noted that plants of *typica* growing on crumbling banks of gullies are sometimes two to three times as large as others only a few meters away but growing in firm, undisturbed soil. This size is doubtless because of better moisture conditions resulting from natural cultivation, subirrigation, and reduced competition.

Furthermore, that there are numerous biotypes is indicated not only by field observation but more certainly by the segregation of these in garden cultures. From some of the wild biotypes, distinct races have been established; they are described in the part of this paper that deals with the genetic study. The results obtained from the comparatively small number of forms tested suggest that the total number of genetic variations possible of segregation were cultures to be made from all parts of the area occupied by the species, would be very large.

1. H. CITRINA Greene, Man. Bay Reg. Bot., 1894, p. 194.—Greene separated this species from *lutescens* by its vernal flowering and by its broader, glandular-pubescent, and not lanate leaves. The concept of *citrina* is of some value if extended to include all of the early flowering specimens of *lutescens*, for these have rather numerous and broad leaves well up the stem as well as at the base, and the heads are mostly larger than in typical autumn flowering *lutescens*. The differences in pubescence mentioned by Greene, it is now recognized, have no taxonomic significance. This is shown in the following series, in which is also noted the narrower character of the leaves of plants developing late in the season.

In Greene's specimens, gathered April 16, 1886, and presumably the types (UC 89003), the leaves are remarkably broad, running from 6 to 12 mm., with an average of 9 mm., but somewhat lanate, especially on the back; in specimens gathered at Tiburon, a peninsula in San Francisco Bay, on May 31, 1909 (*Walker 185*) and May 13, 1915 (*Hall 9896*) the leaves are 2 to 12 mm. wide, with an average of 7 mm. and moderately to copiously lanate; similar specimens were gathered at this station June 13, 1915 (*Babcock*); in specimens from the same locality, July 12, 1915, the leaves are 2 to 6 mm. wide, with an average of 3 mm., and either green or slightly lanate (*Hall 10056*); as the season passes the leaves become too dry and curled to permit of exact measurement. The type locality of *lutescens* is on the east side of the bay and directly opposite Tiburon. Here no spring flowering plants are found, but those blooming from midsummer on have leaves of average width, mostly 4 to 10 mm., and rather copiously lanate (*Hall 9860*, etc.).

Accepting the vernal form as typical of *citrina*, we find it differing from typical *lutescens* in two characters not mentioned by Greene, namely, the leafy stems and large heads. But as in the case of pubescence and width of leaf, we find all stages in one locality as the season advances, for example, Tiburon, the more leafy form being most abundant in the spring, intermediate forms occurring during the summer and passing insensibly into typical *lutescens* in the autumn. Late flowering plants in moist depressions are as leafy as in the spring form but the leaves are green and the heads small. At this Tiburon station the autumn form rather outdoes the majority of the plants at the type locality of *lutescens* in respect to scant foliage and reduced flower size. Judging from numerous collections, the preceding remarks apply to many localities in

Marin County besides Tiburon and to the counties lying to the north and northeast, but the seasonal changes have been closely observed only at that station. It is certain that the great bulk of autumn flowering plants occurring from Marin County to Sonoma and Napa counties are to be considered as genuine *lutescens* rather than the *citrina* variation.

According to garden tests the early habit of *citrina* is at least partially fixed, for seeds gathered at Tiburon, May 29 (184/14) yielded plants in 1915 that were about a month earlier in maturing than plants in the next bed from seeds gathered near San Rafael, October 1 (185/14). In the following season volunteer seedlings in the bed (185/14) where plants of the late flowering form had been grown came up as early as those from beds where there had been only the early flowering form (184/14), but they did not develop so rapidly and averaged nearly a month behind in date of maturity. In this second generation all plants from seed originally brought from Marin County developed ahead of any from seed originally from the east side of the bay. This seasonal difference can be modified by holding seedlings of the early form in boxes until well into the spring and then transplanting into light shade. By this means the development was so delayed that the two forms, now identical in all of their characters, matured at the same time.

Our conclusions from the foregoing considerations are that *citrina* is composed of those individuals of the subspecies *lutescens* which reach anthesis in the spring; that these vernal plants have a tendency to produce broader leaves, to carry these farther up the stem, and to bear larger heads; and that there is a grading off in all of these characters as the season advances, resulting in autumn in normal *lutescens*, a narrow-leaved, very glandular, naked-stemmed, and small-headed form. The lanate character of the pubescence is not seasonal but is too erratic to be of diagnostic value. That the early flowering habit is inherited is proved by the breeding experiments, but such genetic differences are not greater than those obtaining in the case of horticultural varieties. Moreover, it is to be remembered that environmental conditions profoundly modify the time of maturity, the duration of anthesis, and leafage, so that it is sometimes impossible to determine from observation alone whether a particular plant represents an ecologic or a genetic variation. These early and late flowering strains of *lutescens* are exactly paralleled among the forms of *luzulaefolia*, the corresponding white flowered subspecies.

2. H. CONGESTA CALYCULATA, but the achenes as in *Clevelandi*, that is, broader in proportion to their length.—The length to breadth ratio of 6 achenes, as determined for table 1, are 58, 70, 71, 75, 76, and 79 per cent, respectively. The heads are rather more spicate in their arrangement than in *calyculata*, and since the single collection comes from far to the east of the known range of this subspecies a separate origin direct from *Clevelandi* is suggested for this form. In all external features, however, aside from the achenes, it is very much like *calyculata*. The collection was made at Red Bluff, in the Sacramento Valley, California, on September 20, 1892, by *Brandegee* (UC).

3. H. CONGESTA CLEVELANDI, but more villous and less glandular than in the type.—The extreme form, in which the herbage is gray with a long villous pubescence and the glands almost entirely suppressed, is represented by a collection from Glenn County, California (*Heller 11530*). Plants scarcely less villous and nearly as free from glands come from northern Lake County (*Tracy 2319*, *Hall 9502*) and from Trinity County (*Tracy 5217*). These localities lie

to the north of the area of typical *Clevelandi*, but still farther north, especially in Oregon, is again encountered the very glandular form (*Heller 12965*), and from this northern border of the area of distribution of the species come also forms that are exactly intermediate (*Howell, Cusick 2901*). This tendency toward the segregation from *Clevelandi* of two forms differing only in pubescence parallels the development of *Tracyi* from *luzulaefolia*, but the separation has not gone so far, either morphologically or geographically, and therefore their designation as distinct subspecies is perhaps not necessary.

4. H. CONGESTA CLEVELANDI, but the heads few and scattered near the ends of elongated, wand-like branches of an open inflorescence and the pubescence intermediate between that of *Clevelandi* and *typica*.—The bracts of the inflorescence have the peculiar broad bases of the latter subspecies, and the form may be a hybrid between this and *Clevelandi*. The achenes are as in the latter. Collected along the Petaluma and Santa Rosa road, California, August, 1880, *Congdon* (UC).

5. H. CONGESTA LUTESCENS × LUZULAEFOLIA.—This natural hybrid occurs abundantly where the ranges of the parents meet, and its origin has been demonstrated by its production in artificial crosses. The hybrids exhibit all shades of color in the ligules from the yellow of one parent to the white of the other. They have been studied in the field chiefly along the northeast shores of San Francisco Bay. This locality is within the area belonging to *luzulaefolia*, which is here abundant, but directly across the bay to the west is an abundance of *lutescens*. It is probable that seeds of this yellow-flowered subspecies are occasionally blown or otherwise carried across the bay, which is 3 km. wide at San Pablo Strait, and give rise to colonies on the east side. Sometimes, as near San Pablo, the type locality of *lutescens*, these colonies occupy several hectares, but they soon mingle with the white subspecies with the result that there are intervening belts several kilometers wide in which are found an abundance of hybrids of varying shades of yellow.

6. H. CONGESTA TRACYI, but the lower leaves somewhat crowded and those of the middle and upper portion of the stem gradually reduced.—This is a seasonal form which does not come into flower until late July, as may be noted from the citation of specimens under *Tracyi*, where collections belonging to this variation are indicated in the footnote. Similar seasonal variations in leafiness occur also in the subspecies *lutescens* and *luzulaefolia*, as described elsewhere.

7. H. CONGESTA TYPICA × LUTESCENS.—A form growing in eastern Marin and southern Sonoma counties, California, where the ranges of *typica* and *lutescens* meet, exhibits the features of both of these subspecies in varying proportions and is almost certainly a hybrid between them. Its duplication by artificial crossing has been accomplished (p. 58) and in the field it acts exactly like the analogous *lutescens–luzulaefolia* hybrid, the origin of which has been also experimentally verified. The wild hybrids have the general appearance of *typica* and the same broad-based bracts of the inflorescence of that subspecies. The involucral bracts are intermediate, the tips being sometimes moderately longer, sometimes a little shorter than the basal portion. The pubescence around the scattered heads is more glandular than in *typica* and more villous than in *lutescens* and the ligules are pale yellow in color. The hybrid is represented by collections from 10 km. northwest of San Rafael and from about 20 km. northwest of Petaluma (*Hall 10237, 10245*, respectively, UC).

A series of these hybrids, showing various intermediate stages between *typica* and *lutescens*, has been assembled from Leddy Station, between Santa Rosa and Sebastopol, by *McMurphy* and preserved at the Dudley Herbarium of Stanford University.

8. H. CONGESTA TYPICA, but the inflorescence dark with numerous short-stalked glands.—The softly villous, gray pubescence, so characteristic of *typica*, is quite wanting on some plants, more or less prominent on others. The broad-based bracts of the inflorescence, the involucre, and the whole habit are exactly those of *typica*, except that the heads are slightly more scattered. This variation is known from but a single collection made on grassy southwestern slopes facing the ocean, 5 km. south of the point of Cape Mendocino, Humboldt County, California (July 1, 1918, *Tracy 4981*, UC). According to Tracy, it is common here, replacing the smooth form (*Tracyi*) of the interior hills. Although like *typica* in most of its features, the glandular pubescence suggests a possible connection with *luzulaefolia*, or perhaps with *Clevelandi*. But this unusual form will need further field study and garden experiment before its phylogeny can be established.

9. H. CONGESTA TYPICA, but with unbranched stems and the heads all sessile in a short terminal spike.—This reduced form comes from Santa Rosa, (*Heller 5637*, UC) and from El Verano (June, 1888, *Curran*, UC), both in Sonoma County, California. Aside from the features mentioned and the rather narrow, elongated leaves, the form plainly belongs to the subspecies *typica*, of which it is doubtless an ecad.

10. H. RUDIS BENTHAM, Bot. Sulph., 1844, p. 31.—This is the abundant autumnal form of *H. c. luzulaefolia*. It differs from the genuine or spring type of the latter in that it is less leafy, the elongated Luzuloid leaves being confined to the base instead of carried well up the stem as in typical *luzulaefolia*, and the heads are smaller. The relation between these two forms is exactly the same as that between the vernal and autumnal forms of *lutescens*, as described in this enumeration under *H. citrina*. Intermediate forms are common in the herbaria and abundant in the field. The two extreme types sometimes grow together and develop at the same time. Thus in a collection made May 27, 1917, from an area of a few square meters in Contra Costa County, some plants would pass for typical *luzulaefolia*, others for undoubted *rudis* (*Hall 10314*); and in beds of the autumnal form at Richmond, in the same county, occasional plants of the spring type develop simultaneously with their neighbors (*Hall 9878, 8979*). Sometimes the very leafy spring type produces only very small heads, as, for example, collections from Sonoma County made in May and June (*McMurphy*).

In garden cultures it is found that the leafiness and early flowering traits of true *luzulaefolia* are inherited, at least for one generation. But the heads in these cultures are no larger than in those of *rudis* (see also under Size of Heads, p. 25). A complication in regard to leafiness arises from the fact that this feature is strongly influenced by local conditions. Thus seeds of *rudis* produce, in the garden, plants so leafy that they simulate in general appearance the genuine *luzulaefolia*.

From all of the available evidence it seems that *rudis* is the original form and that the less common *luzulaefolia*, which unfortunately was the first to be described, is composed only of those plants which are able to reach maturity during the spring and early summer, when conditions are more favorable for

the development of foliage and heads. This early germination and development may be due either to the genetically precocious nature of certain individuals, or merely to the circumstance that these are especially favored in their early stages and thus acquire a lead over the others. Certain evidence from back-crosses, to be presented later, seems to support the former view (see p. 57). It is not improbable that both causes are operative, and, if so, it is impossible to determine in the field which plants owe their features to genetic factors and which to ecologic. At any rate, the maintenance of a taxonomic distinction between *luzulaefolia* and *rudis* would seem to be without significance.

The nomenclature of these forms has become so complicated that it requires comment. Some workers on the group have assumed that the name *luzulaefolia* was first applied to the common autumn type. There is nothing in the description to indicate otherwise except the doubtful evidence that the leaves are described as elongate-linear *after* both lower and upper leaves have been mentioned and that the Luzula-like foliage is more in evidence in the spring than in the autumn. We have not seen the original specimens in the DeCandolle herbarium, but in the Gray Herbarium there is a sheet labeled "California, Douglas, Benth.," and without doubt a part of the original collection. In this specimen the long Luzuloid leaves, silvery-silky though somewhat dingy, are carried up the stem to the inflorescence, exactly as in the spring type and not at all as in *rudis*, thereby identifying the spring form, sometimes treated as *H. grandiflora* Abrams, as genuine *luzulaefolia*... The autumn form is even more satisfactorily identified as *rudis*, for in the original description of this species Bentham describes the lower cauline leaves as an inch long (*pollicaria*), and after examining the type in the Benthamian Herbarium at Kew, W. L. Jepson wrote in his notes "Late summer state, branches many, long, slender, straight, a slight *suggestion* of racemoseness to the heads. Exactly *luzulaefolia* of the autumn fields."

GENETIC INVESTIGATIONS

Material and Methods

Hemizonia congesta is an insect-pollinated species, the pollen being clumpy, not powdery, and the flowers visited by flies, moths, and doubtless other insects. The individual plant is self-sterile. This was discovered only after numerous efforts to obtain self-fertilized seed from individual plants by enclosing them in cages. Such plants usually produce achenes in abundance, but with exceedingly rare exceptions they are parthenocarpic or abortive. This fact makes the technique of crossing very simple. It is only necessary to protect the heads intended for use as pollen and seed parents by the use of paper bags, the pollen being transferred directly by gently rubbing one head over the other. The self-sterility of the individual plant, however, makes the production of pure lines in the strict sense impossible; but it was found that, by selecting pairs of plants and crossing reciprocally, it was possible to establish inbred strains or races. Seeds

of all the pedigree cultures were germinated in small pots of sterile soil in the greenhouse, usually in January, and transplanted first into flats and later into the garden.

Crosses Between Subspecies

Subspecies cross 1: *rudis* × *citrina*[4] (U.C.B.G.[5] 198/14–7–11 ♀ × U.C.B.G. 184/14–1–4 ♂).—On account of our mutual interest in the taxonomic questions centering in these forms, one of the first experiments was the crossing in 1915 of *H. c. luzulaefolia* (the fall flowering form, which for the sake of brevity will be referred to hereafter as *rudis*) with *H. c. lutescens* (the spring flowering form = *citrina*). The F_1 population, grown in 1916, consisted of 7 plants which were uniform as to stature and habit and intermediate between the parents in size, time of flowering, and color of flowers (ligules), the color being pale lemon yellow fading to cream or, in two of the plants, 16.52–3 and –5, fading nearly to white. The latter plants and two others, 16.52–6 and –7, were chosen for reciprocal crosses and the seed thus obtained produced a combined F_2 population of 181 plants. The most remarkable thing about this population was the great variability among the individuals. All were intermediate between the grandparental types in certain characters and none approached closely to either grandparental type in all characters. This certainly indicates that *citrina* and *rudis* differ in several or many genetic factors.

Considering as one family the cultures grown from reciprocal crossings, there were two families in this F_2 population, and between these two families there was an interesting difference in the variation in flower color, although the great majority of the plants in both families bore flowers of an intermediate tint of light yellow. Unfortunately,

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[4] These are not subspecific names but are applied to genetic strains, or at the most to natural biotypes occurring within particular subspecies. The following tabulation may assist in placing the variations:

Subspecies	Minor variations, including strains and biotypes
(1) *lutescens*	(*a*) *citrina*, an early developing form.
	(*b*) genuine *lutescens*, a late developing form. (Additional strains derived from *citrina* are listed in the table, p. 64.)
(2) *luzulaefolia*	(*c*) genuine *luzulaefolia*, an early developing form.
	(*d*) *rudis*, a late developing form.
(3) *typica*	(No distinction made between early and late developing forms.)

[5] University of California Botanic Garden. The first two numbers, 198/14, indicate accession number and year, the next is the row number, and the last, the plant number. After the first year the page number of the annual notebook and the plant number, connected by a hyphen, were used.

the exact flower color of the two *grandparents* was not recorded, but the absence of special notes in the record certainly indicates that the *rudis* plant was typical of the subspecies in color of ligules, i.e., a yellowish or greenish white (about 25g or 26g of Ridgway),[6] while the ligules of the *citrina* plant were almost certainly lemon chrome (21). All of the F_1 plants were pale lemon yellow (23b) fading to cream, except that two of the plants, 3 and 5, faded to nearly white. As records were made of only the extreme color variants in the F_2 population, the data are unfortunately incomplete; but it is noteworthy that among the 70 progeny from reciprocal crossings of 16.52–3 and –5 there were 3 plants whose flower color was recorded as 25g, probably about as light as typical *rudis*, while among the 111 progeny of 16.52–6 × –7 there were 5 recorded as 23f or g, which would be described as pale cream or creamy white. These F_1 and F_2 results would seem to indicate that the *citrina* grandparent was heterozygous for one of several pairs of factors affecting color of the ligules, an assumption which is strengthened by the study of flower color in *citrina* (p. 78).

This F_2 population is shown in plate 3, figure 1, as culture number 17.84, and in the same figure appears a row of *rudis*, 17.77, and a row of *citrina*, 17.76. As all of these cultures were sown at the same time and treated in the same way, the genetic differences in time of maturity are clearly indicated. In plate 3, figure 2, two cultures are shown: 17.92 is the backcross of the F_1 with *citrina* (pedigree: 16.52–3 ♀ × 16.3–1 ♂ and reciprocal, the parents of 16.3–1 being the same *citrina* plant that was used in 1915 for the original cross with *rudis* and U.C.B.G. 184/14–1–1, another very similar *citrina* plant); 17.96 is the backcross of the F_1 with *rudis* (pedigree 16.50–11 ♀ × 16.52–3 ♂, the parents of the *rudis* plant, 16.50–11, being U.C.B.G. 198/14–7–8 and an unidentified *rudis* plant). The uniformly near approach of these two backcross populations to the respective grandparental types is clearly shown, i.e., the backcross with *citrina* closely resembled *citrina*, and the backcross on *rudis* closely resembled *rudis*, not only in time of maturity but in other characters, notably flower color. This, of course, is what would be expected in view of the evidence from the F_2 population that the two subspecies differ with respect to numerous characters. As regards ligule color in particular, in the first backcross there were no plants with flower color lighter than picric yellow (23d), and the color ranged from that to lemon chrome (21), the

[6] Numerical designations of color refer to Ridgway (1912).

color typical of *citrina*. In the backcross on *rudis* there were 16 plants in the family, of which only one had flowers as dark as 23c, while two plants had cream ligules (23e?), and in the other 13 the color was the greenish or yellowish white of *rudis* (25g). It was noted above that the F_2 segregation indicates that one of the grandparents, probably the *citrina* plant, was heterozygous for one pair of genes affecting flower color. This population from a backcross on *rudis* gives additional evidence favoring such an inference.

Subspecies cross 2: *citrina* × *typica* (16.15–1 ♀ × U.C.B.G. 87/15–1–1 ♂).—The *citrina* plant used was not related to the one crossed with *rudis* in the preceding case. It happens that 16.15–1 was an unusually robust, late-maturing plant selected from the variable progeny of two rather robust *citrina* plants found in the Botanic Garden culture of 1915. Its flower color is not known, but it was certainly as dark as lemon yellow or darker. The *typica* plant was one of a fairly uniform culture grown in the Botanic Garden in 1916; and *typica*, it will be recalled, is a spring flowering form. The F_1 population, 17.104, shown in plate 3, figure 4, consisted of 8 vigorous plants of early or medium early maturity like *typica*, and resembling that form in habit and foliage. The flower color of 5 of these plants was recorded as: 23, 23a, 23b, 23d, 23e; records lacking for the other 3. The 2 F_1 plants having flower colors 23 and 23b were reciprocally crossed and produced an F_2 population, 20.254, 255, consisting of 32 plants which displayed notable variations in habit as well as in flower color and time of maturity. Of the 32 plants, 20 were early or medium early in maturity, 9 were medium late, and 3, late. The flower color records obtained for 19 of these plants may be summarized thus: 2 (23a or b) + 3 (23d–f) + 2 (23f) + 7 ('tinged white') + 5 ('white'). In all likelihood the last class had ligules as 'white' as those of *typica*, the flower color of which has not been recorded in terms of Ridgway's *Standards*. Here again the F_1 population indicates heterozygosity probably in the *citrina* grandparent, while the F_2 distribution is such as might result from segregation and recombination of one or two pairs of genes according to the arbitrary grouping of the five classes recorded above. Finally, it should be noted that the cotyledons of these F_2 plants showed a general resemblance to the cotyledons of *typica* and that the mature plants had the *typica* characteristic of conspicuous leaves surrounding the heads, although somewhat variable in this. Thus in a cross with *citrina* several *typica* characters tend to be dominant. This is not necessarily, however, an indication that

typica is the more primitive form; indeed, its ability to become established as a distinct subspecies may be due to this dominance.

Subspecies cross 3: *typica* × *rudis* (U.C.B.G. 87/15–1–1 ♀ × 16.49–18 ♂ and 16.49–10 ♀ × 87/15–1–1 ♂).—The same *typica* plant was used as in the previous cross. The two *rudis* plants were very similar sibs in a remarkably uniform family of 24 progeny of the two earliest flowering *rudis* plants in the first garden culture. Like their parents, they were all of early maturity for *rudis*.

The F_1 families, 17.99 and 101 (pl. 3, fig. 3), consisted of 8 and 11 plants, respectively, and the combined data as regards time of maturity are as follows: 3 early, 7 medium early, 8 medium, 1 medium late; but it should be noted that these classes are relative, that they were made with reference to spring flowering forms, and that those classed as "medium" came into flower earlier than did their *rudis* parents. The flower color was noted as similar to *rudis* or *typica* with slight variations. No F_2 progenies were grown. The absence of any pronounced color in the flowers of the F_1 plants, however, is significant, especially when considered in connection with the fact that each subspecies, when crossed with *citrina*, gives colored F_1 progeny and a minority of white flowered plants in F_2. This indicates that both of these subspecies differ from *citrina* in lacking something essential for flower color. Whether the two are genetically alike in this respect cannot be known from these data, but from the data on flower color in *citrina* this would appear probable.

The results from crossing subspecies are of general significance in that they demonstrate the crossibility and interfertility of these particular subspecies and indicate to some extent the actual genetic relationships of the forms crossed. Thus there is evidence of segregation, and hence of Mendelian inheritance, of flower color and time of maturity as well as such characters as size and habit of plant. These artificial hybrids, together with the wild specimens already described as natural hybrids, furnish abundant proof that free interbreeding is general throughout this whole group of forms. This in itself is a strong argument in favor of treating the group as one species.

Genetics of H. congesta lutescens

Variation, selection, and inbreeding.—The first garden culture (1915) of the spring flowering form, *citrina*, consisted of about 300 plants, grown from wild seed collected at a single locality near

Tiburon. This population was noticeably more variable than adjacent cultures of *lutescens* and *luzulaefolia*, and it was therefore seized upon as the most favorable for genetic experiments. There was striking diversity in size, vigor, and habit of plant, width of basal leaves, pubescence of basal leaves, color of foliage (shades of green), color of ray-flowers (two tints of yellow), and color of anther-tubes in disk-flowers. Ten pairs of plants were selected with reference to one or more of the foregoing characters, in most cases the two plants being as closely similar as possible, and were crossed reciprocally. In this way 18 families were grown in 1916; 10 of these families were fairly uniform and resembled their 5 pairs of parents more or less closely, while 8 families, representing the other 5 pairs of parents, were notably variable. Pairs of similar plants were again selected, in all cases both plants being in the same family or reciprocal families, and intercrossed, thus giving 16 inbred strains, some of them represented by several families, in 1917.[7] Certain of these strains will be described. It should be noted here that the work was interrupted in 1917 by the world war, and the next cultures were grown in 1920.

Effects of inbreeding.—As would be expected in a species exclusively cross-fertilized, close inbreeding even for a single generation produced marked effects. The most striking of these effects are presented in the order of their appearance.

1. Intersterility between plants of certain families.—The original 10 pairs of plants which were intercrossed in 1915 all produced viable seed, giving families containing from 1 to 27 plants the next year. As a result of brother-sister intercrossing in 1916, seed was obtained for 44 families. In 1917 there were 12 of these families which failed completely to germinate. It must be noted here that caged individual plants produce seed which fails to germinate and which upon examination is found to consist merely of empty shells. It is probable that these 12 lots were of this nature, but if any seeds with embryos were present they failed to germinate. The lots contained from 7 to 150 'seeds.' Now it is found upon tracing their pedigrees that these 12 lots came from 8 of the original 10 matings. In the next generation, 1920, seed was sown for 117 families but only 57 materialized. Of the 60 families failing entirely in seed germination, 36 were *reciprocal* families, i.e., they were the progeny of 18 different pairs of plants. On tracing the pedigrees of these 36 families it is found that 14 were

[7] For the sake of convenience these strains were given the descriptive Latin names which appear in table 3, but these names need not be taken into account in applying the rules of botanical nomenclature.

derived from 4 of the same 8 original pairs of plants mentioned above, while the remaining 22 trace back to just one other pair of great grandparents. This indicates that genetic factors (genes) for intersterility between individual plants exist in the wild plants of this subspecies; and, as similar but even more striking results were obtained with *rudis*, such factors probably occur throughout the species. (See also under Segregation.)

2. Lethal and semilethal seedling characters.—Albino seedlings which died in the cotyledon stage appeared in 4 families in the first inbred generation, and in one family (17.56) 5 out of 11 seedlings had yellowish green cotyledons; 2 of these died, 3 developed and were included in the garden culture, and only 1 reached maturity. Of these 5 strains throwing seedlings defective in chlorophyll, 3 were derived from one pair of grandparents and the other 2 trace back to another pair. Albino seedlings are occasionally produced from wild seed.—Retarded and abnormal seedlings appeared frequently in the first and second inbred generations (F_2 and F_3 from original crossings). Such retarded plants are shown in plate 4, figure 5, in which the arrow indicates the most abnormal one in which there is failure of differentiation in the plumule, and a secondary growing point is forming in the axil of one of the cotyledons. Several other types of abnormality were noted. These defective seedlings predominated in closely related families, most of them occurring in the *lacteandra* strain which descended from a single pair of grandparents.

3. Segregation in inbred strains.—That even those original pairs of similar plants, which produced fairly uniform F_1 families, actually differed with respect to certain genetic factors is clearly shown by the sharp segregation found in F_2 from brother-sister matings in F_1. Thus the parents of the *lacteandra* strain, C16–5 and C18–6, while differing somewhat in habit, were similar in other respects and produced rather uniform F_1 families, as shown in plate 4, figures 1, 2, 3. All 6 F_2 families, expected from intercrossing 3 different pairs chosen from 9 F_1 plants, were realized, but of the 24 pairs of F_2 plants which were crossed reciprocally, only 13 pairs produced families, while the achenes from the other 11 pairs failed to germinate. The pedigree of this strain and the segregation in F_2 are shown in table 2. The ratio of the classes of F_2 families is 1:1, from which it appears that one parent was heterozygous and the other homozygous for a gene which causes intersterility only when both plants involved in a cross are homozygous for it. Thus if *a* represents the gene in question and *A* its dominant

allelomorph, the grandparental cross was $Aa \times aa$, giving 1 Aa:1 aa in F_1. Each of the three F_1 pairs must have resembled the parents in genotype, again giving in F_2 a 1:1 ratio. The selection of F_2 pairs of plants for intercrossing was made with reference to color of anther-tubes. Of the F_2 families that failed, 6 were purple × purple, 3 were cream × cream, and 2, purple × cream. Thus, so far as the intersterility factor was concerned, the selection of F_2 plants was quite at random, resulting in the 1:1 ratio of families realized to families that failed. Since the 11 F_2 pairs which failed to reproduce when crossed reciprocally were derived from a single pair of grandparents, they comprise an intrasterile class, comparable to classes known to occur in *Nicotiana, Veronica, Linaria,* and *Bursa.* See review of recent literature by Anderson (1924).

In this connection we note that there is evidence of a low percentage of self-fertility or pseudo-fertility in individual plants of this species. A plant of the *nana* strain, 16.2–6, was bagged for crossing but some of the bags were not removed until harvest, when they were found to contain a total of 220 achenes. These were sown as culture 17.107 and 4 plants resulted. These plants were bagged in order to test them for self-fertility with the following results: 17.107–1 gave 29 achenes, of which one germinated and produced a very small plant (about 8 dm. high); 17.107–2 gave 64 achenes but none germinated; 17.107–3 gave 268 achenes, of which two germinated but only one plant developed, reaching a height of 17.5 dm.; 17.107–4 gave 33 achenes and none germinated. So in this strain there is a slight tendency to self-fertility. Also, during 1917, 213 selfed achenes were obtained in the same way from 12 other plants representing 5 other strains. Only one of these germinated, but it produced a plant which resembled its parent closely, and it was doubtless the result of self-fertilization. Hence there is a small amount of self-fertility in these plants at the height of the season; whether it increases as the season advances is not known.

As regards habit of plant, C16–5 was homozygous for 'erect' branches and C18–6, for a 'spreading' factor. All of the 6 F_2 families from this original cross showed segregation into strictly erect, semi-erect, or half-spreading, and spreading[8] plants, but it was sometimes difficult to distinguish between semi-erect and spreading individuals. Matings of strictly erect F_2 plants produced large F_3 families of strictly erect plants, illustrated by plate 4, figures 4*a*, 4*b*. But the

[8] This should not be confused with *procumbens* habit.

F_3 families from semi-erect and spreading plants gave variable results. One family of 8 plants obtained by crossing spreading F_2 plants is shown in plate 4, figures 5*a–h*. The garden notes on habit were as follows: 5*a* semi-erect, 5*b* spreading, 5*c* strictly erect?, 5*d* strictly erect, 5*e* semi-erect, 5*f* semi-erect, 5*g* (?), 5*h* spreading?. The 3 retarded plants were so small that they could not be classified with certainty, but as this population was produced by *spreading* plants, and as the semi-erect type shows a tendency to breed true, while crossing erect with semi-erect produced spreading in F_1, the latter must be a heterozygous condition. Another spreading type, designated *brevicaulis-procurrens*, first selected in 1915, has never bred true but always segregates into two or three types. Still another habit type which seems to be the expression of a heterozygous genotype is *arborella*, illustrated in plate 6, figure 3, since several such plants have produced segregating populations. However, as several factors may be involved in these cases, it is, of course, possible that, with sufficiently large numbers, true-breeding individuals might be selected.

TABLE 2

SHOWING PEDIGREE AND SEGREGATION OF F_2 RECIPROCAL FAMILIES INTO THOSE WHICH GREW AND THOSE WHICH FAILED EVEN TO GERMINATE

P_1	F_1	F_2 reciprocal families		Total F_2 families
		Grew	Failed	
			17.62–14x15	
	16.27– 1x 3	17.62– 2x10	17.62– 9x19	
	– 3x 1	17.62– 1x 8	17.63– 1x 9	
			17.63– 5x 7	
		4 families	8 families	12
		17.64– 5x10		
		17.64–13x16	17.64–14x23	
C16–5	16.27– 8x10	17.64–21x22	17.64–15x17	
[illegible] x	–10x 8	17.64– 4x 6	17.65– 6x38	
C18–16		17.65– 8x10	17.65– 9x11	
		17.65– 1x 7		
		12 families	8 families	20
		17.66–15x20		
		17.66–22x27	17.66–17x35	
	16.30– 1x 2	17.66–41x42	17.66–43x44	
	– 2x 1	17.66–45x46	17.67– 5x 6	
		17.67– 1x 7		
		10 families	6 families	16
	Totals.....	26	22	48

TABLE 3

Pedigrees of Eleven Inbred Strains of Citrina Showing Average Height of Plants in Centimeters (Italicized) in Each Generation

Number of plants measured stated in parentheses

1915—P_1	1916—F_1	1917—F_2	1920—F_3	Strain
C 6– 7 x C17–17 (2) *47.5*	16.15–1 x 16.28–30 (2) *25*[a]			
C 2– 5 x C 2– 9 (2) *60*	16.6–1 x 16.7–1 (2) *54*	17.34, 35 (19) *37.5*	20.129,130,131,132, 134,135 (107) *17.5*	*stricta*
C 2–17 x C 9–16 (2) *42.5*	16.8 (3) *25*	17.42,43, 44 (10) *27.5*	20.80,82,86, 87,88 (50) *20* 20.86 (6) *27.5*	*limona*
C16– 5 x C18– 6 (2) *31*	16.27 16.30 (9) *31*	17.62,63,64, 65,66,67 (61) *31*	20.28 to 20.79 (227) *17.5*	*lacteandra*
C 6– 3 x C 9– 7 (2) *32.5*	16.14 (4) *35*	17.49,50, 51,52 (17) *31*	20.9,10,12, 16,17 (30) *24* 20.10 (4) *31*	*argentea*
C 3– 8 x C14–17 (2) *27.5*	16.10–1x4 (2) *36*	17.46 (8) *32.5*	20.4,5,6 (31) *17.5*	*procumbens*
C 1– 4 x C 1– 1 (2) *36*	16.10–5 x 16.3–2 (2) *35*	17.29 (4) *47.5*	20.24,25 (42) *25*	*brevicaulis-procurrens*
	16.3–2 x 16.2–2 (2) *30*	17.24,25 (5) *37.5*	20.20,21,22 (96) *21.5*	
C 1– 3 x C 2–18 (2) *34*	16.2–3x10 (2) *32.5*	17.41–2x3 (2) *17.5*	20.92 (31) *25*	*nana*
C 1–14 x C 9– 6 (2) *65*	16.5–3x4 16.18–1x3 (4) *52.5*[a]	17.36,37 17.56,57 (14) *55*	20.94,96 *robusta I* 20.100,101,102, 103,104 (127) *37.5* *robusta II* 112–123 *robusta-supera* av. for 112–123 = *50*[b] av. for 100, 101 = *45* av. for remainder = *35*	
C10– 1 x C 8– 4 (2) *24*	16.21 (4) *46*	17.60,61 (4) *36*	20.164,166 (3) *32.5*	*subrobusta*

[a] May be slightly in error.

[b] Some of these were enormous plants, 120–150 cm. in diameter.

Segregation into types in the inbred strains was accompanied by reduction of variability, particularly with respect to the characters for which the original selections were made. Thus in the *argentea* strains, derived from one of the 10 original pairs which were chosen because of their silvery pubescence, there was segregation in F_2 with silvery plants in the minority; but, by crossing F_2 silvery plants, uniformly silvery F_3 families resulted. At the same time there was a general tendency toward reduction of variability in the inbred strains, which would no doubt have become more marked, could inbreeding have been carried farther.

4. Reduced vigor in inbred strains.—Of the original 10 pairs of plants selected in 1915, one had no progeny in F_2, but each of the others gave rise to one or more distinct strains, some of which received Latin names for the sake of convenience. As height of plant was measured in at least part of the individuals in every family in each generation, we have an index of the reduction of vigor resulting from inbreeding. Although but few individuals were measured in the F_1 and F_2 generations, yet in every case the individuals figuring in the pedigree were included, and the results are so consistent throughout the 9 strains that the mean height alone can be used as a basis for comparison between strains. In table 3 the reduction of vigor resulting from two generations of inbreeding is clearly shown. In 5 of the strains the average height decreases progressively from generation to generation, and in all the strains the average height of the F_3 families is less than the average height of the two great-grandparents, the reduction being most marked in the case of *stricta* and *limona*. The rather marked *increase* in mean height of the F_2 plants in *brevicaulis-procurrens* is obviously due to the difference in pedigree, for in this case the F_2 families have four grandparents instead of only two as in the typically inbred strains. This is perhaps heterosis of the type shown by Jones' double F_1 crossed corn (Jones, 1922). The increase in F_3 as compared with F_2 in the case of *nana* is easily explained as due to the small population in F_2, and the small size of the 2 plants in question may have been due to segregation of genes for size. An obvious result of such segregation is found in the marked differences in height between F_3 families within certain strains, particularly *limona*, in which family 20.86 averaged 27.5 cm. as compared with the general average of 20; *argentea*, in which family 20.10 averaged 31 cm. as compared with the general average of 24; and *robusta*, in which family averages of 35, 45, and 50 cm. occurred. Thus, in general, inbreeding

caused reduction in vigor in all of the strains, this reduction being more marked in some strains than in others, while certain F_3 families are as vigorous as their parents or even their great-grandparents. These exceptional F_3 families doubtless result from the segregation of genes in F_1 and the recombination of certain genes (perhaps some of them being complementary genes) which were segregated to the particular F_2 plants used as parents of F_3. These results seem to parallel those of King in inbreeding white rats (King, 1918), where weak individuals were avoided in matings and thus genes for vigor were concentrated. The same may have occurred as a matter of chance in these tarweed selections. Most, if not all, of these robust strains, however, would doubtless have suffered some reduction in vigor, could inbreeding have been continued; but from the few *robusta* crosses it was possible to make in 1920 no viable seed was obtained. In the 3 inbred strains which were continued until 1921 the situation was similar. Seed was obtained for 12 families, of which two produced 1 plant, one produced 2 plants, and one 4 plants; these plants were very small and weak.

5. Heterosis.—Realizing in 1920 that the inbred strains were failing to reproduce themselves, crosses were made between several strains, giving seed for 14 hybrid families. All but 3 of these lots of seed produced progeny, and, although the families were small, due to limited amount of seed, the plants were vigorous and set seed abundantly. Similar results came from a few strain crosses made in 1917 in studying the inheritance of certain characters; the large size of some of the families thus obtained and the vigor of the plants in others was noted. This enhanced reproductive ability is the best evidence we have of heterosis in strain crosses. Comparison of height of plants in crosses and inbred strains in 1921 is out of the question because of unusual environmental conditions and paucity of data. In 2 of the strain crosses grown in 1920 the average height of the F_1 population slightly exceeded the midparental height, but in the other 2 there was a decided falling off in vigor, due presumably to the fact that the strains had been inbred for only one generation and that the plants crossed, though larger than the average, were heterozygous. It thus appears that, besides those causing cross-sterility, there are other genes affecting reproduction directly, and that these are present but masked in the wild plants and cause rapid degeneration of inbred strains.

6. Adult abnormalities.—Some of the reproductive factors just alluded to manifested themselves in abnormal floral structure in several inbred strains. Most striking was the occurrence of virescence and prolification of the flower-heads as described in a previous paper (Babcock, 1924). In such heads the disk-flowers, which normally produce the pollen, are completely metamorphosed into vegetative structures. Other floral abnormalities observed in inbred strains were changes in number of lobes on the ligules and modification in form of the ligulate corolla. The ligulate corolla is normally 1-lipped, but one of the *stricta* families in 1920 contained several plants with 2-lipped ligules. The added posterior lip stood erect, thus forming a crown surrounding the disk-flowers, as in the collarette type of Dahlia. Petallody, or the occurrence of small petal-like structures, borne within and attached to the tube of the corolla, was noted in several inbred strains (Babcock, 1924). Both the collarette character and petallody are inherited. Another abnormality, more clearly defective in nature, was absence of the normal purple color in the anther-tube of the disk-flowers. This occurred in one plant of the first garden culture and its inheritance was studied (see p. 73). These morphological abnormalities and defects strongly suggest that genes which exert deleterious physiological effects may also be present in the wild plants, and the evidence of cross-sterility and the degeneration of inbred strains confirm it. These germinal defects are emphasized because of their evolutionary significance. There are other abnormalities, of course, which are due to environmental factors.

Discussion of inbreeding effects.—Thus we find that inbreeding has brought to light numerous deleterious genes which exist in the normal wild plants of this species. These results remind one of the effects of inbreeding in maize (Shull, 1908, and East, 1908), and they resemble Collins' results from inbreeding *Crepis capillaris* (Collins, 1920), except that the latter species does not possess so many deleterious genes, presumably because there is a certain amount of self-fertilization in *Crepis capillaris*. But these are very different results from those reported on hemp (Fruwirth, 1922). Although closely inbred for six years or more only two conspicuously abnormal plants appeared, which were sterile females. Hemp is a dioecious species, but it has been long under cultivation, during which time it has been subjected to artificial selection for desirable characters. From our results with a wild species, however, it seems that natural selection does not

eliminate defective germ plasm (recessive genes which condition lethal, semilethal, or defective characters). On the other hand, it may play an important rôle in the establishment and spread of new and better adapted types which arise from time to time through mutation and recombination of genetic factors. We shall refer to this point again.

Clearly, the distinct types which were isolated through inbreeding were not a result of cultivation. Their prototypes existed in the first garden generation, grown from wild seed. Furthermore, the defective characters which came to light during the experiments were not induced by culture but were merely the expression of recessive genes present in the wild plants. Due to the natural method of reproduction in this highly specialized species, they may have been in existence for a long time, but they must have originated by genic changes or mutation in the narrow sense, and in all probability they arose independently of the environment.

The robusta strain.—This strain is worthy of special attention because of its interesting history and the remarkable types which it has produced. The two original plants were equally robust, both reaching a height of 65 cm., and similar in minor characters, such as color of foliage, nature of pubescence, width of leaves, length of leaves, and number of rays per head, but they differed in habit in that C1–14 had a long central axis with comparatively short, stout stems, while C9–6 had a shorter axis and the branches were longer, especially the lower ones. The presence of anthocyan pigment in C1–14 was indicated by purple coloration of the healthy leaves, while it seemed to be absent in C9–6. Both were about a month later in flowering than the earliest *citrina* plants. The 6 F_1 plants resulting from reciprocal crossings all resembled C9–6 in habit, as is shown in plate 5, figure 3. This plant, 16.18–1, was crossed reciprocally with 16.18–3, thus producing an F_2 population (17.56, 57) of 13 plants, some of which were truly remarkable. One of these, 17.56–5, reached a height of 55 cm. and developed long lower branches forming a broad conical bush about 120 cm. in diameter (see pl. 5, fig. 7), and 17.56–2 was similar but grew only 45 cm. high. These were crossed in the hope of establishing a new strain. But the results, as shown in plate 5, figure 8, were disappointing, as none of the 23 plants (20.100, 101) were of this widely spreading type; instead they were more like C9–6 and the F_1 hybrids. Another F_2 plant (17.56–4) was outstanding because of its height, 80+ cm., its habit which resembled C1–14, and

its late maturity, as it did not flower until after July 1, whereas some strains began flowering on June 1 of that year. This plant was remarkable, too, for its very dark green color, due to anthocyan as indicated by purple coloration of the leaves; also because of virescence and prolification of the flower-heads as mentioned above. The most similar plant in the population was 17.56–7, which grew 55 cm. high and was dark green, but differed somewhat in habit and commenced flowering June 8 (see pl. 5, figs. 4 and 5). In crossing these two plants P_4 was used only as ♀, due to defective disk-flowers. The result was 13 F_3 plants, 4 of which are shown in plate 5, figure 6. One of these (20.123–7) resembled 17.56–4 as it appeared when fully grown, and some of the flower-heads were virescent. There were 4 others which approximated this type and like it were late flowering and highly vigorous. They began flowering about July 1 and on September 9 they were still growing and blooming, although they had had no water since June. The remaining 8 were decidedly earlier in maturity, more slender, less leafy, and, so far as observed, showed no virescence of disk-flowers whatever.

While these data are not sufficient to warrant any definite hypothesis concerning the genes involved, the history of the strain certainly indicates that the two original plants differed or were heterozygous with respect to genes determining habit and time of maturity, and that some *citrina* (spring flowering) plants carry genes for late maturity and the robust, leafy habit developed by *rudis* under garden conditions (pl. 7, figs. 2, 3). This point will be referred to again. The presence also of genes which lowered cross-fertility is indicated by the difficulty in obtaining viable seed throughout the history of the strain. A total of 60 heads or about 700 individual florets were hand-pollinated under bag in order to secure 6 viable seeds of the original cross. There is no record of the number pollinated in F_1, but in F_2 in making the one cross, 17.56–4 × 7, 35 heads or about 400 florets were pollinated and only 13 F_2 plants resulted. It appears that the genes conditioning excessive vegetative vigor in this strain are in some way antagonistic to reproduction, but entirely independent genes that happen to be present in the two grandparental genotypes may be responsible. There is, of course, the possibility that this outstanding strain was cytologically distinct, perhaps tetraploid, but the fact that *rudis* has the same number of chromosomes as *citrina* makes this less probable.

Several characteristics of the *robusta* strain remind one of the indeterminate growth type of tobacco which originated as a mutation some years ago (Jones, 1921). It was shown (Garner and Allard, 1920) that this type of tobacco as well as many other plants is governed by the relative length of day and night. "When the day is artificially shortened, the new type of tobacco flowers and sets seeds normally in the summer." Jones concludes that this indeterminate growth type originated through mutation in a single gene. It may be that the seasonal differences between genuine *lutescens* and its *citrina* form, also between genuine *luzulaefolia* and its *rudis* form, are dependent upon a very few genes conditioning response to relative length of day. That there is heterozygosity within each subspecies for length of life or time of maturity has been demonstrated.

Inheritance of four characters in citrina.—1. Procumbent habit. The original plant of this type, had it not displayed the procumbent character, would have resembled the other rather small, semi-erect, early flowering plants which made up a large portion of the first *citrina* culture. But the procumbent habit was very striking in appearance and it was observed that the stem and branches were just as wiry and strong as in erect plants. The procumbent habit evidently was not due merely to weakness of the supporting tissue in the shoots; it was a true reversal of geotropic response in stem and branches. After the plant was found, search was made for another like it, but without success. Accordingly, it was crossed with C3–8, which was used as ♀ parent, and these, together with one of the 12 F_1 plants, are shown in plate 6, figures 1, 2, 3. The F_1 plants were all upright in habit except one, which was of the very short-stemmed, spreading type called *brevicaulis-procurrens* and not at all like the procumbent parent. Of the others, 6 were of the type shown in 16.10–1, and 5 were smaller, erect, and branched from near the base like C3–8. Unfortunately, only 2 of the F_1 plants were crossed, 16.10–1 × 4, with the result that the F_2 population (17.46) consisted of 11 plants, 3 of which died while still very small; of the remainder 4 resembled the parents and 4 the procumbent grandparent. These plants being small and the number of flowers available for crosses quite limited, it was thought wise to attempt only two types of crosses, viz., to treat the procumbent plants as two pairs, so as to see whether what was expected to be the homozygous recessive form would breed true, and similarly to treat the erect plants as two pairs, in the hope that at least one pair would give a segregating population. The former

expectation was realized but not the latter. One pair of procumbent plants produced reciprocal families (20.5 and 6) of 10 and 20 plants, respectively, and all 30 individuals exhibited the procumbent habit, although in a few, which were retarded and small, the exhibition was limited to a distinct bending of the axis toward the ground. Two of the most typical plants of this population are shown in plate 6, figure 4. The other two procumbent F_2 plants and one pair of the erect plants failed to produce progeny. From the other pair of erect plants only one erect offspring was obtained.

Fortunately, it was realized in 1917 that this strain should be outcrossed in order to insure the further testing of this character, so one of the F_2 procumbent plants was crossed with a *robusta* individual (17.36–15). From this reciprocal cross 2 F_1 families were derived (20.137, 138) containing 18 plants, all erect. Four pairs of these were crossed in the hope of getting a large F_2, but two of the pairs failed to produce progeny. The other two pairs produced (21.54, 55, 56) a combined population of 9 plants which were classified as 7 erect and 2 procumbent, a 3:1 ratio. The history of this experiment is summarized in figure 3. In view of the fact that procumbent segregated out apparently as a simple recessive in the second F_2 population, we may consider the anomalous F_2 of 1917 as merely an unusually wide deviation from the normal type of distribution due to the small size of the population, and infer that procumbent habit is conditioned by a single recessive gene. That it is almost certainly conditioned by a nuclear element and not by cytoplasmic constituents is shown by the fact that, in the original cross between procumbent and erect, the procumbent plant was used only as a male.

Our special interest in this character and its inheritance centers in the fact that some biologists assume that such differences in plant habit are merely modifications due to environmental factors, or, if transmissible from generation to generation, that such transmission may be cytoplasmic (plastid inheritance) rather than chromosomal. It is not strange that such easily modifiable characters as number, size, and direction of growth of a plant's branches should be considered as primarily influenced by the environment, especially by those whose viewpoint is that of ecology rather than genetics. As for the rôle of the cytoplasm in geotropism, recent experiments (Small, 1920, 1922) on the reversibility of geotropic response in stem and roots of many plants clearly indicate that certain cytoplasmic constituents, probably proteins, initiate the necessary changes in rate of cell growth.

But this has no bearing on the rôle of the nucleus in controlling cell metabolism. The fact that geotropic response is abnormal under abnormal environment is no more significant genetically than the fact that abscission is induced by subjecting a plant to coal gas. On the other hand, in view of the demonstration that procumbent habit is a Mendelizing character in *Hemizonia*, we may fairly infer that normal

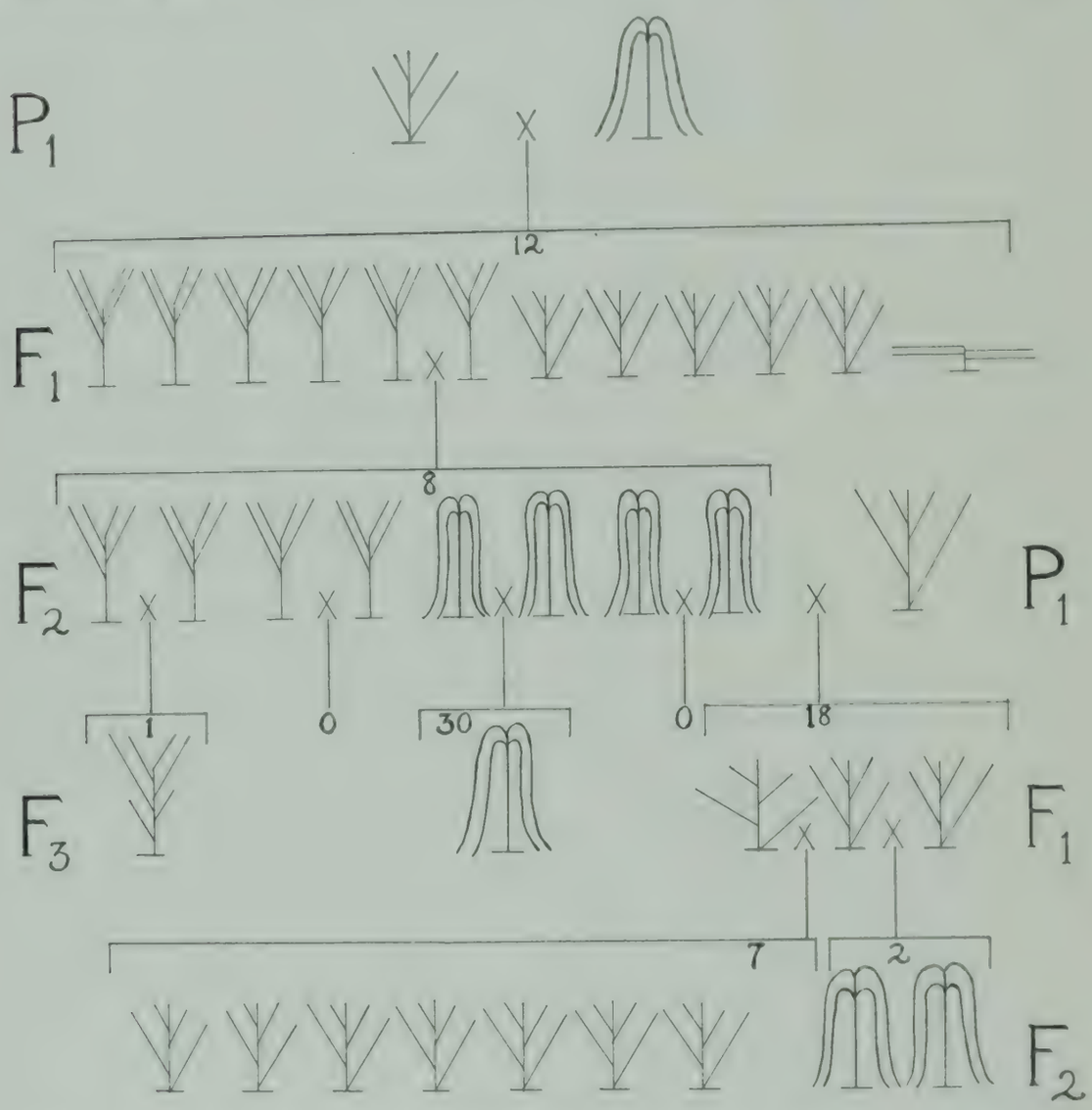


Fig. 3. Chart showing inheritance of procumbent habit in *citrina*. The habit types are indicated diagrammatically. The symbol × indicates a mating between two individuals, and immediately below each × is given the number of progeny from that mating.

geotropic response in plants is primarily dependent upon nucleus rather than cytoplasm. Furthermore, the sporadic occurrence of fastigiate and 'weeping' habits among the higher plants suggests that such types originate by mutation. The demonstration that procumbent habit is a Mendelian character strengthens such an assumption.

2. Cream anther-tubes.—The deep purple anther-tubes of the disk-flowers of this species are so conspicuous in mature heads that a single plant which lacked the purple color was soon noticed. In this plant (C18–6) the anther-tubes were cream in the young flowers and turned to light brown with age. Crossing it with C16–5 produced a combined F_1 population (16.17, 30) of 9 plants, all of which had purple anther-tubes. Three pairs of F_1 plants were intercrossed and produced 6 F_2 families, which segregated in the proportions shown in table 4. This distribution is well within the limits of probability, assuming that cream is conditioned by a single gene, as such a deviation would be expected to occur 28 times in 100 trials under the law of chance. (The probable error, expressed in number of plants, is calculated from the formula, $E = 0.6744898 \sqrt{p\,q\,n}$, in which n is the total number of individuals and p and q are the percentages corresponding to the ratios concerned. See tables of Probable Errors of Mendelian Ratios, issued in mimeograph form by the Department of Plant Breeding of Cornell University.)

As a further test, 52 crosses of F_2 plants were made as follows: 30, purple × purple; 17, cream × cream; and 5, cream × purple or purple × cream. Only 19 of the expected families were realized, due to cross-sterility of certain plants. Of these 19 families, there were 2 from crosses of purple × purple, one with 60, the other with 30 plants, which were all purple, showing that the 4 F_2 plants involved were homozygous for the gene for purple. Seven other families from crosses of purple × purple, ranging in size from 2 to 10 plants were entirely purple, but these families were too small to warrant any inference as to the genotypes of the parents. There was also one family from a cross of purple × cream which contained only 2 purple plants. Then there were 4 families from purple × purple crosses which segregated into purple and cream and these are included in table 4. Here again the distribution is within the limits of random sampling. Finally, there were 5 families recorded as crosses of cream × cream, 3 of which gave all cream in F_3 (a total of 22 plants), showing that those F_2 cream plants were homozygous. The other 2 were reciprocal families (20.63, 64), consisting of 4 plants each. All of these had purple anther-tubes!

This last result was, of course, entirely unexpected and is sufficient to raise a question as to the accuracy of the records or the technique of crossing. There seems to be no reason for doubting the accuracy of the records, and, although an assistant was employed in hybridiz-

ing, the work was very carefully and systematically performed. The original record of crosses kept by the hybridizer has been preserved, and it shows that the cross called for by the records (17.66-15 × 20) was made. Furthermore, the fact that this was a reciprocal cross, involving the transference of pollen from each parent to the other, reduces the possibility of experimental error, and the further fact that the resulting families are alike in having purple instead of cream anther-tubes, argues for the accuracy of the records. Finally, no other questions have arisen concerning records or results which would tend to cause suspicion as to accuracy or technique.

TABLE 4

Proportion of Plants with Purple and Cream Anther-tubes in F_2 and Those F_3 Families Showing Segregation

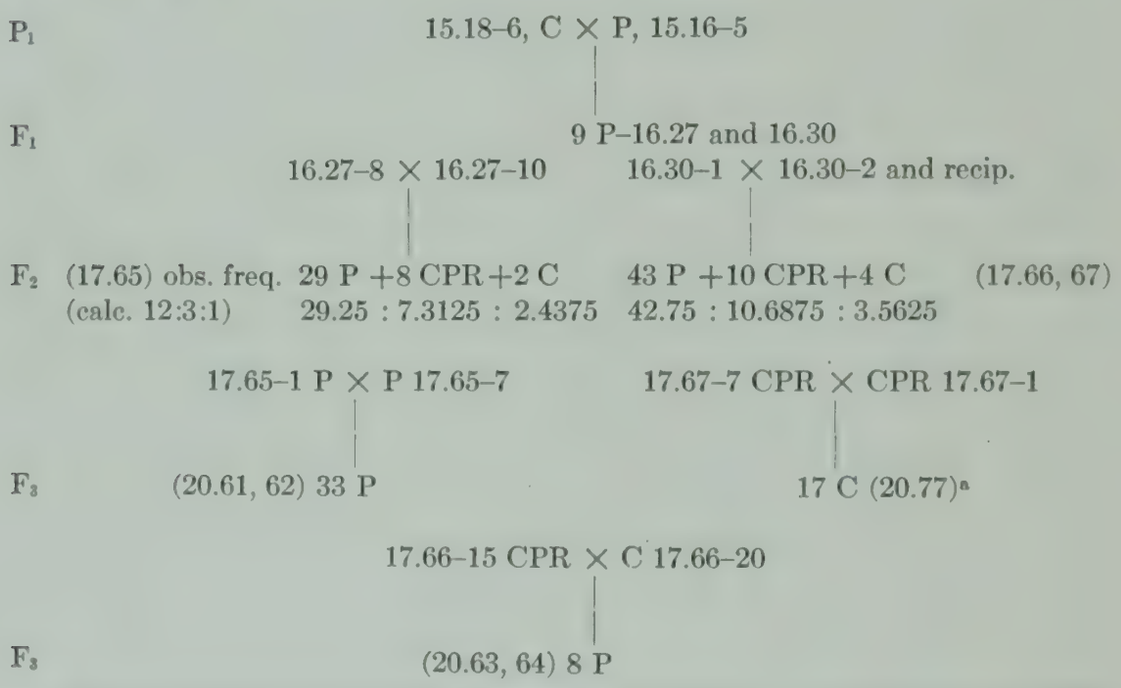
F_1 Cross	F_2 Family	Purple	Cream
16.27– 1 x 3	17.62	17	3
16.27– 3 x 1	17.63	6	3
16.27–10 x 8	17.64	23	2
16.27– 8 x10	17.65	30	10
16.30– 1 x 2	17.66	37	8
16.30– 2 x 1	17.67	6	6
Total		119	32
Calculated 3:1		113.25	37.75
Deviation		5.75±3.59	
D/E=1.8; Probability per 100=28.05			

F_2 Cross	F_3 Family	Purple	Cream
17.62– 2 x10	20.28	11	1
17.62–10 x 2	20.29	42	9
17.62– 1 x 8	20.32	6	.....
17.62– 8 x 1	20.33	1	1
Total		60	11
Calculated 3:1		53.25	17.75
Deviation		6.75±2.46	
D/E=2.7; Probability per 100=6.86			

The original field notes contain the following data. When recording the anther-tube color of F_2 plants in 1917, in the fourth family examined it was noted that many, but not all, of the cream plants had a light tinge of purple confined to the ridges of the tube. All of the cream plants in that family were noted with reference to this character, also in the two families yet to be recorded, but the cream plants of the first three families were not rechecked with reference to purple ribs. Considering only the three families which were rechecked for variation among cream plants, the distribution was 72 purple + 18 cream with light purple ribs + 6 cream, which is exactly a 12:3:1 ratio. Now, one of the two cream plants that produced the 8 purple F_3 progeny had light purple ribs and the other did not. This suggests the possibility that the F_2 plant described as "cream with purple ribs" was in reality a pale purple, possibly heterozygous for the purple gene. But this is negatived by two facts; first, no variation in degree of purple among plants classed as purple was observed; second, the 3 F_3 families consisting only of *cream* plants were the progeny of 4 F_2 plants *recorded as cream with purple ribs.* It seems, therefore, that the segregation of F_2 creams into two classes in the proportion 3:1 was due to a second independent gene for light purple ribs which was present in the purple grandparent. Since the light purple ribs would not be noticed on purple anther-tubes, the 12:3:1 ratio would result. As no notes were taken in F_3 on occurrence of purple ribs on anther-tubes of cream plants, we have no data to support this assumption. But even if such data were available, it would not explain the 2 F_3 families of *purple* plants derived from F_2 cream plants. The presence of an inhibiting or modifying gene would not have produced the 12:3:1 ratio and would have disturbed the 3:1 ratio actually observed. Elimination of all other causes leaves only mutation as a plausible explanation of this case. As cream undoubtedly arose from purple by mutation, it is not unreasonable to expect reversible mutations sooner or later. Such mutations have been reported in *Drosophila* (Morgan et al, 1923) and *Lychnis* (Shull, 1911).

It is of some interest to note the conditions under which this mutation must have occurred. It may have been in either of the two plants, and it must have occurred prior to formation of the flowers, since both pollen and ovules carried purple. Yet the epidermis of the plant was not affected, otherwise the anther-tubes would have been purple. This means that the mutation took place rather early in the life of the plant and in a cell so located that the epidermis was not

affected, although the sub-epidermal layer, from which the germ cells develop, possessed the gene for purple. This is similar to a case reported in *Nicotiana* (Clausen and Goodspeed, 1923), except that in the latter the epidermis only was affected by the mutation so that the mutant character was not inherited. Although the F_2 plants, 8 in number, were all purple, this number is too small to prove that the F_2 plant in question was homozygous, so it is not necessary to assume mutation in more than one gene. Unfortunately, none of these F_3 purple plants were tested as to their genotype for purple. The pedigree of the *lacteandra* strain, including only that portion of the F_2 in which segregation was recorded among the cream plants, is given in figure 4.



[a] No records were made as to occurrence of light purple ribs on anther-tubes in this family.

Fig. 4. Pedigree of part of *lacteandra* strain with observed and calculated ratios. (Note: P = purple anther-tube; CPR = cream anther-tube with light purple ribs; C = cream anther-tube.)

3. Color of ligules.—In the majority of the plants in the first garden culture of *citrina* the ligules were deep yellow (Ridgway 21, "lemon chrome," 21½ or 22), but some of the original selections had "lemon yellow" rays (Ridgway 23). That the yellow color of the ligules in *lutescens* is due to a plastid pigment was shown by microscopic examination of freshly cut sections of ligules. In lemon chrome (21) rays the bright yellow chromoplasts were abundant, being most numerous in the basal third of the upper epidermal cells but occurring also in the lower epidermis and mesophyll. There was no

yellow sap. In the next color grade examined (22) the bright yellow chromoplasts were present chiefly in the epidermal cells. It was estimated that there were more than 100 in some of the upper epidermal cells. In lemon yellow (23) rays the chromoplasts were not quite so numerous as in 21 and 22. In still lighter ligules (23d) the same bright yellow plastids were present but relatively rare, many epidermal cells lacking them entirely. Thus variation from darker to lighter tints of yellow is due to reduction in number of chromoplasts in the cells.

Starting with lemon yellow rays in some of the original pairs of *citrina* plants, further segregation occurred in some of the inbred strains giving still lighter tints of yellow. For example, in one F_3 family (20.88) containing 8 plants, the distribution according to color (Ridgway's numbers) was as follows: 1 (22) + 4 (23) + 2 (23e) + 1 (23f). The lightest of these (23f) is a very pale tint of yellow. One of the plants classified as 23e, when crossed with a plant of another family (20.73–2) which was classed as 23c, produced 10 plants (21.36) which segregated as follows: 2 (23) + 2 (23b) + 1 (23d) + 5 (23f). One of the 5 lightest plants was crossed with a plant (21.48–16) having lemon yellow rays (23). The 72 plants resulting from this cross were distributed as follows: [2 (22½) + **16** (23)] + [8 (23a) + 8 (23b) + 2 (23c)] + [2 (23d) + 7 (23e) + 9 (23f)] + [**16** (23g) + 2 ("nearly white")]. This distribution is clearly bimodal with the 2 modes on 23 and 23g, and with an intergrading series of classes. From this it appears that 21.48–16 was heterozygous for a pair of genes conditioning color and that the 23f plant was a homozygous recessive for the same pair of genes. Incidentally, the population can with good reason be treated as composed of four equal classes, indicated by brackets, which would show that 21.48–16 was heterozygous for two pairs of genes for which the 23f plant was homozygous.

Again, a plant with lemon yellow rays (20.88–8) was crossed with one having lemon chrome rays (20.130–16) and the F_1 progeny (21.48) consisted of 12 (22) + 5 (22½) + 3 (23). The three lightest plants were removed, as well as all other *Hemizonia* plants, so as to allow the 17 classed as 22 and 22½ to set an abundance of seed with the aid of insect pollination, this being a safe procedure as there were no wild tarweeds in the vicinity. An F_2 population of 2302 plants was grown in 1922. The distribution in color classes was as follows: 15 (21) + 23 (21½) + **1560** (22) + 301 (22½) + 263 (23) + 71

(23a) + 15 (23b) + 8 (23c) + 3 (23d) + **23** (23e) + 17 (23f) + 3 (23g). Again we have a bimodal distribution with the modes indicated by heavy type (see also table 5). It is important to remember that the F_1 parents were of two phenotypes as to color (12 plants of color grade 22 and 5 of grade 22½). These plants were close together in an isolated group and were all in bloom at the same time, so that the chances of crossing between any two of them were practically equal. Assuming an equal amount of crossing among the F_1 plants and dividing the F_2 population into two groups comprising classes 21 and 23c and 23d to 23g, inclusive, the calculated ratio, on the basis of a single factor difference, is 534:10, while the observed ratio is 533.1:10.9. We infer from the available data that at least one pair of genes conditions ligule color, and it seems probable that one or more other pairs of genes have a modifying effect on the degree of yellow color, but this question must be left for further investigation.

Since the yellow color of the ligules in *lutescens* depends upon the presence of chromoplasts in the cytoplasm of certain cells, it might be expected that transmission of color from parent to offspring would not follow Mendelian rules. The data submitted indicate that it does, however. Furthermore, some of the crosses gave results that cannot be explained on the basis of cytoplasmic inheritance (assuming that there is no transmission of cytoplasm through the pollen). There were two crosses between plants with very pale yellow ligules which resulted in some progeny with rays of a deeper tint of yellow. That color of ligules depends primarily upon nuclear elements, genes, is clear.

4. Collarette ligules.[9]—In one of the F_3 families of the inbred *stricta* strain (20.130, 131) 4 out of 31 plants possessed some of the collarette rays mentioned under inbreeding effects. The new character appeared with no regularity, nearly every head having some collarette rays in one plant, while in others such rays were more rare, some heads lacking them entirely. One of these 4 plants, 20.130–16, was crossed with 20.88–8 for the double purpose of studying color inheritance and inheritance of collarette. The 20 F_1 plants had no collarette rays whatever. Of the large F_2 population only 10 per cent displayed collarette rays, and the number of such rays per plant varied from every ray in all the heads to only one in 417 rays. That

[9] In the work on both ligule color and collarette rays the authors are indebted to Mr. C. Wm. Haney for painstaking assistance in collecting and reducing the data.

the distribution of collarette rays parallels closely the distribution for ligule color is shown in table 5, which indicates the independent inheritance of collarette. The appearance of this character in 13 per cent of the plants of an inbred family, its disappearance in F_1, and its reappearance in 10 per cent of the F_2 progeny, are taken to indicate that collarette is conditioned by a single gene which is recessive to a gene for the normal, one-lipped type of ray. The erratic expression of this gene when present in homozygous condition may be due to various conditions, concerning which it would be useless to speculate without further experiment.

TABLE 5

DISTRIBUTION OF PLANTS WITH COLLARETTE LIGULES IN THE VARIOUS COLOR CLASSES OF AN F_2 POPULATION

Color	Color frequency	Collarette	
		Observed frequency	Calculated relative frequency
21	15	3	1.6
21½	23	3	2.5
22	1560	163	167.4
22½	301	32	32.3
23	263	24	28.2
23a	71	13	7.6
23b	15	1	1.6
23c	8	1	0.9
23d	3	1	0.3
23e	23	2	2.5
23f	17	3	1.8
23g	3	1	0.3
	2302	247	247

DISCUSSION OF RESULTS FROM GENETIC STUDIES

Evolution within the species.—That mutation plays a rôle of primary importance in the evolution of this group is strongly indicated by several lines of evidence. Reasons have been given for considering *lutescens* the most primitive of all the subspecies in the group. We now have additional evidence from the results of inbreeding in *citrina,* the spring flowering form of *lutescens.* In the *robusta* strain, for example, all of the inbred plants were larger, more vigorous, and much later in flowering than plants which would be considered typical of *citrina.* In one F_2 family of this strain in particular,

several plants appeared which were recognized as *rudis*-like because of their stout, semi-erect branches arising from near the base of the plant and because of their late maturity, all these features being characteristic of *rudis* as it appears in garden cultures.[10] These plants are shown in plate 7, figures 2 and 3, in comparison with typical *rudis* and *citrina* plants. In the same plate, figures 5 and 6, two plants of genuine *lutescens* are shown, the one being a *rudis*-like, late flowering individual, and the other an earlier flowering type, like *citrina*. Furthermore, the appearance of *citrina* plants with ligules so light as to be classed as *rudis*-like is a further indication of the potentialities of this subspecies. In other words, within *lutescens* we find the ability to produce forms characteristic of *luzulaefolia*, the subspecies which includes *rudis* as a minor variation, and the differences between these forms are such as might be expected to originate through changes in genes. The tendency toward dominance of *typica*, when crossed with *citrina*, does not weaken the hypothesis that *lutescens* is the most primitive subspecies. On the contrary, it is just those rare mutations that result in greater vigor or better adaptability, which would tend to be preserved by natural selection, as has been pointed out (Morgan, 1923).

Additional evidence that the evolution of this group is accomplished, at least in large part, by mutation is found in the fact that several characters, some of which are of a fundamental physiologic nature, such as those affecting reproduction, have been shown to be inherited according to the general Mendelian principles. Hence, there can be little doubt that inheritance in this group is based primarily on genes, and genic differences arise by mutation. Furthermore, there is some evidence that mutations are occurring from time to time in these plants. Besides the case of plants with purple anther-tubes from reciprocal crosses between two plants with cream anther-tubes (p. 76), there were several other instances not yet mentioned. In 1920 there was a single plant with very pale lemon yellow rays (23c) in a pedigree culture of an inbred strain, which had produced only lemon chrome (21), or near lemon chrome flowers, for three generations. This case was apparently due to a change in one gene affecting flower color. Two sporadic cases of plants in which the flower-heads were completely virescent may also have been due to mutation. In one of these plants all the flowers were virescent, but the branches

[10] Wild plants of *rudis* are typically leafy at base, but garden conditions cause a greater development of the upper leaves, as shown in the illustrations

on one side of the plant were several inches longer than those on the other side (Babcock, 1924). This chimerical condition suggests vegetative mutation.

There are the further facts that our cytological data, although scant, certainly indicate that all the subspecies have the same type of chromosome group; also, that no cases of inheritance or mutation have arisen which cannot be explained in terms of one or more pairs of genes. In short, mutations in the sense of genic changes, together with the recombination of characters continually occurring through cross fertilization, have furnished the genetic variability needed for evolution in this group. Natural hybridization between subspecies may also produce new types from which still other subspecies are developed. For example, the subspecies *calyculata* is treated in this paper as probably having arisen in this manner. But the other natural hybrids which we have observed and studied experimentally are all intermediate and apparently transitory. At any rate, the genetic variability of *lutescens* can be accounted for without resort to hybridization.

The possibility of the origin of new forms in this species by a process of gradual modification by the environment, as contrasted with mutation, has been given careful consideration. All that can be said in regard to this is that we have been unable to find positive evidence of such origin, except in the case of evident ecads easily and gradually reversed by environmental changes. Although the possibility of an origin through gradual modification and isolation cannot be positively disproved, it seems unnecessary to assume the existence of such a process in the present case, where mutation has been demonstrated as so common a phenomenon.

The bearing of these studies upon evolution.—The evidence here presented on the genetics of three subspecies of *Hemizonia congesta* calls for their consideration as very similar groups of genes which yet differ with respect to numerous individual genes. It has been shown that a primary evolutionary process in these plants is mutation in the narrow sense or, in other words, the germinal variations which make evolution possible in this case are changes in individual genes. The cause of these changes is not known. Although the environment may have something to do with it, it certainly is not the result of garden culture, for there are numerous recessive abnormalities and lethals now existing in the wild plants. Similar deleterious mutations are known to be of common occurrence in *Drosophila,* and thus far it has not been possible to establish any casual relation between such

mutations and known environmental factors. The theory of evolution through chance mutation and natural selection (Morgan, 1919) seems to hold good in the case of these tarweeds.

Natural selection in this cross-fertilized species does not eliminate defective germ plasm (recessive genes which condition lethal, semi-lethal or defective characters) except as homozygous recessives are eliminated, for the tendency is to maintain the highest possible degree of heterozygosity. On the other hand, natural selection must play a tremendously important rôle in preserving new forms arising through occasional, rare, progressive mutations which induce some gain in adaptability. There must be good reasons why *luzulaefolia* (especially the *rudis* variation) has the widest geographic distribution of all the subspecies, while *lutescens* is restricted to certain limited areas. A strong indication at least as to the basic reason is found in the greater vigor displayed by *rudis* under garden conditions. Furthermore, that *luzulaefolia* developed from *lutescens* as a result of mutations and natural selection is all but demonstrated. At the same time isolation by natural barriers must be an important, perhaps the deciding, factor in the establishment of such subspecies as *Clevelandi, calyculata*, and *Tracyi*. At any rate it is difficult to imagine that any gain in adaptability would accrue from the morphological changes which distinguish the latter two from the other subspecies, and they occur in more or less isolated areas. These three subspecies are evidently younger than *typica* and *luzulaefolia*, and, as they are less widely distributed, they conform to Willis' theory of "age and area." But when we compare *luzulaefolia* and *lutescens* as to distribution, the situation is reversed, for here the younger form has much the wider distribution. Hence, in this species at least, Willis' theory does not hold as regards either age and area or the evolutionary processes at work.

SUMMARY

1. An attempt has been made to synthesize from widely divergent sources evidence relating to the evolution of a small but complex group of organisms. This evidence has been derived from studies in genetics, cytology, ecology, comparative morphology, and geographic distribution.

2. The problem has been viewed from the standpoints of the geneticist, the ecologist, and the field taxonomist. There has been a general agreement in results, although on some points it has been necessary to recognize two hypotheses, neither of which could be definitely proved.

3. The numerous possible character combinations have led to a large number of natural forms, some of which have previously been classed as distinct species. All of the forms are so closely tied in by intergradations and by hybrids, and the genetic behavior of all is so similar, that the entire assemblage is treated as one taxonomic species, namely, *Hemizonia congesta*.

4. The comparative morphology of the minor forms reveals the existence of natural assemblages within the species. Six of these are sufficiently well set off through reduction in the number of intergrades to justify their recognition as subspecies.

5. The subspecies are roughly correlated with geographic distribution, but there is overlapping along the borders. Here also occur intermediate forms which are probably natural hybrids.

6. No differences have been found in number or individuality of the chromosomes. Only subspecies *typica*, *luzulaefolia*, and *lutescens* have been examined.

7. The most primitive subspecies appears to be *lutescens*, from which two principal branches have been developed, one passing through *typica*, the other through *luzulaefolia* (chart, p. 32). This conclusion is based upon genetic evidence (pp. 79–82) and upon the principles of phylogeny (p. 23).

8. The three remaining subspecies have not been investigated genetically, but the principles established for the others assist in the placing of these.

9. Units smaller than subspecies are described as minor variations (pp. 50–55). Garden forms of known genetic origin are classed as strains and designated by monomials (p. 64).

10. Artificial hybrids are easily produced, and in some cases they duplicate the supposed natural hybrids. Free interbreeding is general among all of the subspecies tested. Hybridization does not usually lead to permanent forms, but such an origin is suggested for subspecies *calyculata*.

11. Individual plants are self-sterile. Hence the highest possible degree of heterozygosity exists in nature, and many wild plants carry recessive defects in their germ plasm.

12. Inbreeding, in general, caused reduction of vigor, but in certain inbred strains the vigor, as indicated by size of plant, was not reduced in the third generation, while it was actually increased in one F_3 family.

13. Inbreeding of certain forms of *lutescens* resulted in the production of plants with the characteristics of *luzulaefolia* (*rudis* form). This is additional evidence that the former is the more primitive.

14. The results from crossing *luzulaefolia* and *typica* with *lutescens* also strengthen the inference that the last is the most primitive subspecies. The dominance of certain *typica* characters in such a cross and the greater vigor of *luzulaefolia* as compared with *lutescens* in the garden are consistent with the hypothesis that both *typica* and *luzulaefolia* developed from *lutescens* through progressive mutations.

15. Certain morphological and physiological characters are shown to be inherited according to Mendelian principles. Numerous other hereditary variations appear to have originated through mutation. Gradual modification by the environment is not believed to result in distinct genetic types in this group, but environmental stimuli may be the unknown causes of germinal changes. The variations leading to evolution in this species, in so far as investigated, are changes in individual genes.

16. Natural selection of favorable mutations adequately accounts for the origin of five of the subspecies, while the geographic distribution of three of these forms indicates that isolation has been a factor in establishing them.

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EXPLANATION OF PLATES

PLATE 1

Hemizonia congesta calyculata. Type specimen in the Herbarium of the University of California.

Fig. 1. Upper branch. × 1.

Fig. 2. Head with subtending leaves. × 2.

Fig. 3. Ray-corolla (white). × 4.

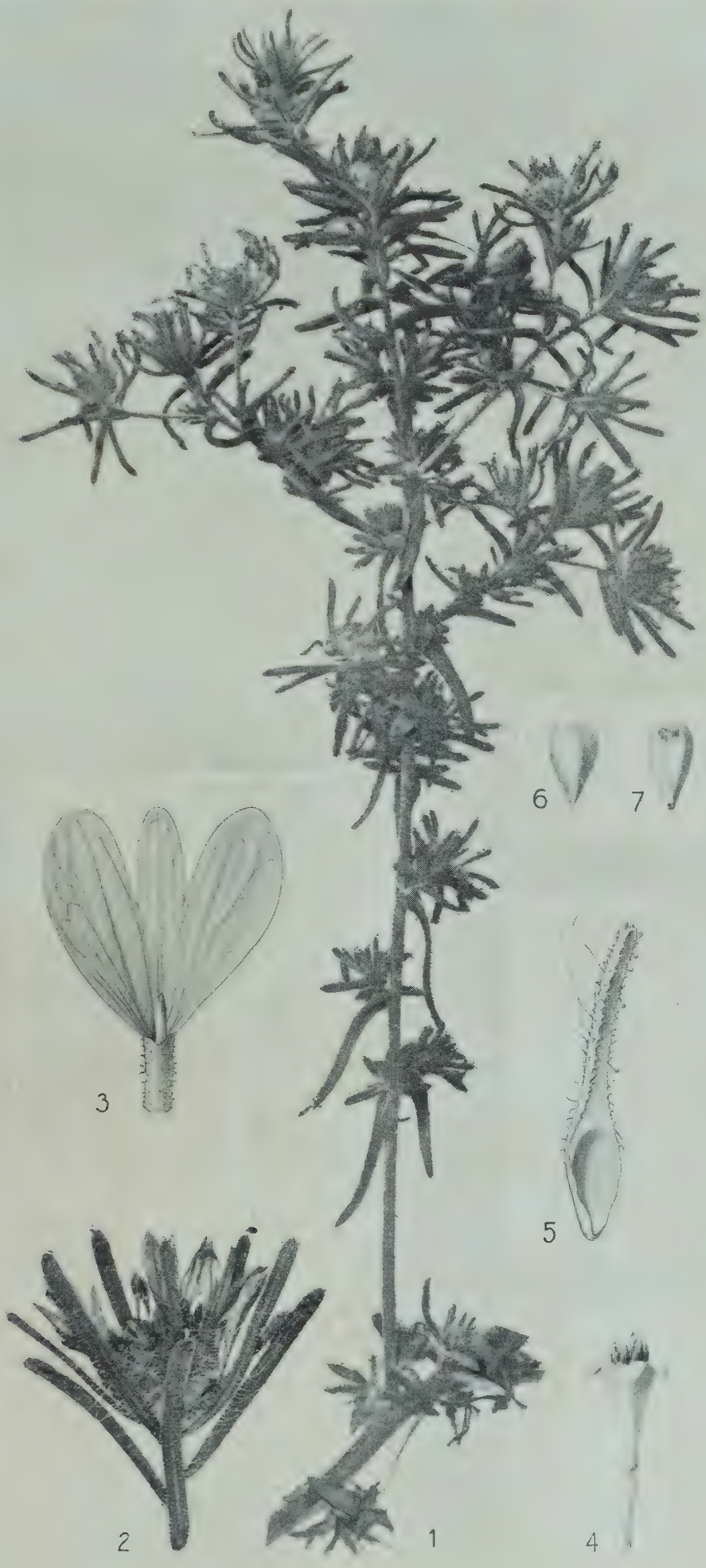
Fig. 4. Disk-flower. × 4.

Fig. 5. Bract of the involucre after removal of the achene. × 4.

Fig. 6. Back view of ray-achene. × 4.

Fig. 7. Front view of another ray-achene. × 4.

Figures 1 and 2 from photographs by W. C. Matthews; figures 3 and 4 from drawings by Helen Rearwin; figures 5, 6, and 7 from drawings by Anna Hamilton.


6
7
3
5
2
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4

PLATE 2

Hemizonia congesta Tracyi. Type specimen in the Herbarium of the University of California. × 0.4.

From a photograph by W. C. Matthews.

Plants of Northern Coast Ranges of California
CENTIMETERS

PLATE 3

Hemizonia congesta. Crosses of subspecies.

(The names here used represent biotypes not given taxonomic status. *Citrina* is a form of *H. c. lutescens; rudis* is a form of *H. c. luzulaefolia; congesta* is *H. c. typica.* See also under Minor Variations, pp. 50–55.)

Fig. 1. 17.66. A row of *citrina* plants in full bloom, being a portion of an F_2 population from the cross, cream × purple anther-tube.

17.77. A row of *rudis* plants of same age.

17.84. The F_2 population, several rows, from the cross, *rudis* × *citrina,* made in 1915.

Fig. 2. 17.92. A row of plants from the backcross (F_1 *rudis* × *citrina*) × *citrina.*

17.96. A row of plants from the backcross (F_1 *rudis* × *citrina*) × *rudis.*

Fig. 3. 17.99. F_1 *congesta* × *rudis.*

Fig. 4. 17.104. F_1 *citrina* × *congesta.*

1

2

3

4

PLATE 4

Hemizonia congesta lutescens. Inbred strains of the spring flowering form, *citrina.*

Fig. 1. This plant (C18–6) was selected from the first garden culture in 1915 because it had cream anther-tubes and was intercrossed with the plant shown in figure 2.

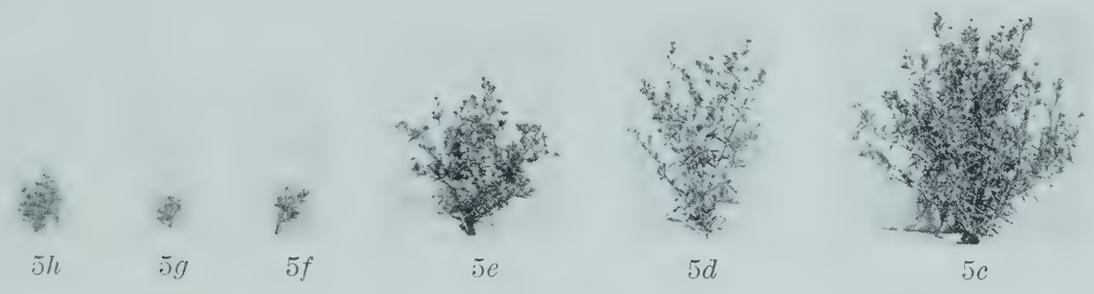
Fig. 2. This plant (C16–5) had purple anther-tubes and, although similar to C18–6, differed from it in branching angle, the branches being more nearly vertical.

Fig. 3. One of the two F_1 families (16.27); the reciprocal (16.30) consisted of two similar plants.

Figs. 4*a*, 4*b*. Two F_3 plants (20.43–51 and 50) derived from two erect plants (P_{12} and P_{16}) of an F_2 family (17.64) which showed sharp segregations into erect, semi-erect, and spreading plants. The 61 plants of 20.43 were all erect like the ones shown here.

Fig. 5. Another F_3 family (20.70) in seedling stage. Note one precocious, four intermediate, and three retarded plants.

Fig. 5*a–h*. The same family at maturity—5*a* is the precocious one, 5*b–e*, the intermediates, and 5*f–h*, the retarded ones. The segregation in size is remarkably sharp. In habit, 5*c* and 5*d* are erect, 5*a* and 5*e* semi-erect, and 5*b*, spreading, while the other three are too small to classify. This family is the progeny of two low spreading plants (like 5*b*) of an F_2 family (17.66) which also showed segregation into erect, semi-erect, and spreading plants.



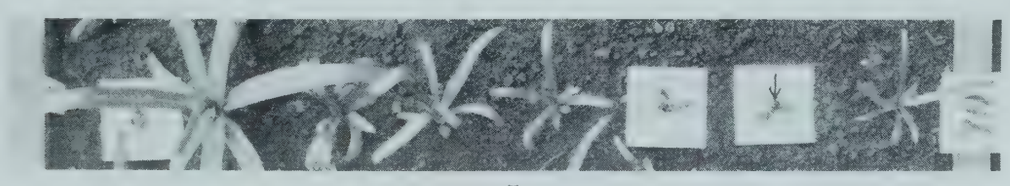


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PLATE 5

Hemizonia congesta lutescens—the *robusta* II strain.

Figs. 1, 2. These plants, C1–14 and C9–6, were selected in 1915 for intercrossing because, although differing somewhat in habit, they were both strikingly robust, reaching a height of 65 cm. when mature.

Fig. 3. One of the six F_1 plants (16.18–1) resulting from reciprocal crossings. It reached a height of 60 cm., and the other five plants were closely similar, only varying somewhat in size. Crossed with 16.18–3, a remarkable F_2 family was produced.

Figs. 4 (17.56–4) and 5 (17.56–7). Two of the 13 F_2 progeny. P_4 reached a height of 82 cm. and was still growing, while P_7, which was of somewhat earlier maturity grew 55 cm. high. These were crossed to start a new strain (see fig. 6).

Fig. 6. Four of the 13 F_3 plants resulting from crossing 17.56–4 and 7. Although the average height of this family was only 50 cm., some of the plants were enormous, measuring 120 and 150 cm. in diameter (cf. fig. 7).

Fig. 7. Another F_2 plant (17.56–5) which was remarkable for its widely spreading lower branches. It was crossed with a similar sib in the hope of establishing a distinct strain, but see figure 8.

Fig. 8. Two of 23 similar plants in the progeny of 17.56–5 × 2.

C1-14

1

16.18 P1

3

C-9-6

2

17.56 P4

4

17.56 P7

5

20.123 P7
20.112 P2

6

17.56 P5

7

20.100
1
2

8

PLATE 6

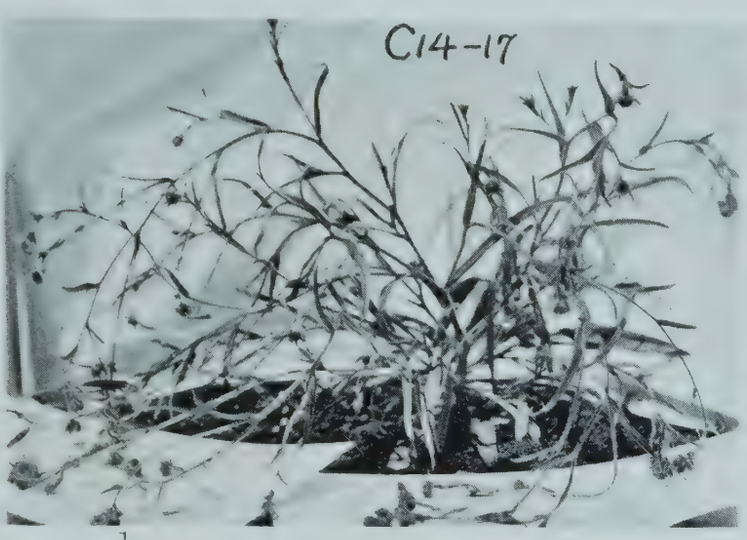
Hemizonia congesta lutescens. Inheritance of procumbent habit.

Fig. 1. The first procumbent plant (C14–17) and the only plant in the first garden culture exhibiting this character.

Fig. 2. This erect plant (C3–8) was crossed with the procumbent plant in order to study the inheritance of the procumbent character.

Fig. 3. One of the 12 F_1 plants from the cross C3–8 ♀ × C14–17 ♂. These plants were all upright in habit except one, and this was of the *brevicaulis–procurrens* type, not *procumbens*. Of the others, six were like the one shown here, 16.10–1, and five were branched from near the base and erect like one parent. P_1 was crossed with P_4, a similar but somewhat smaller plant.

Fig. 4. Two of an F_3 family (20.5) of 30 procumbent plants, obtained by crossing two F_2 procumbent individuals. No photographs of the F_2 generation were obtained.



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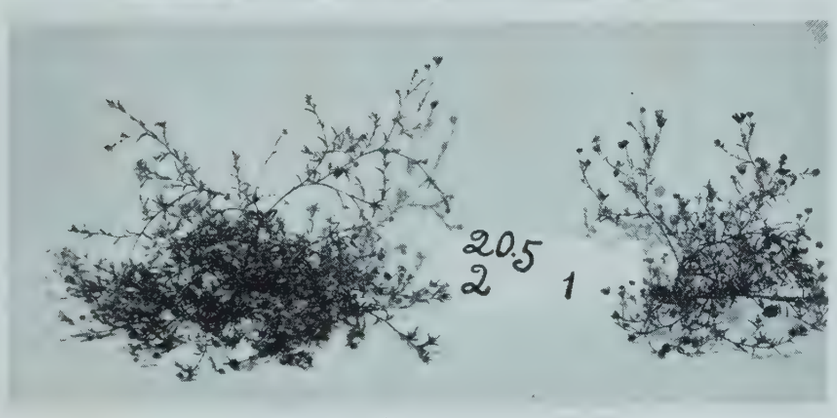

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PLATE 7

Hemizonia congesta

Fig. 1. *H. c. luzulaefolia,* a young plant of the fall flowering form, *rudis.*

Fig. 2. A *rudis*-like *citrina* plant, 17.56–9, of the *robusta–supera* strain.

Fig. 3. Another *rudis*-like plant, 17.57–4, of the same strain.

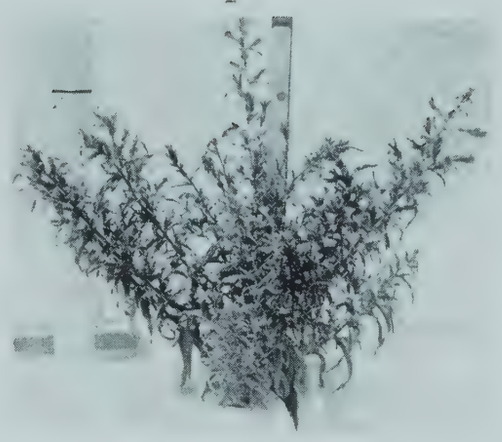
Fig. 4. *H. c. lutescens,* a *citrina* plant, C2–5, fairly typical of this form as grown in the garden.

Fig. 5. *H. c. lutescens,* a young *rudis*-like plant, L8–16, of the fall flowering form, more leafy than in wild plants.

Fig. 6. *H. c. lutescens,* a *citrina*-like plant, L4–2.

1

2



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NOTES ON MICRODICTYON

BY

WILLIAM ALBERT SETCHELL

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NOTES ON MICRODICTYON

BY

WILLIAM ALBERT SETCHELL

For some years I have realized that the current statements concerning the genus and species of *Microdictyon* were confused and misleading, and having to consider carefully the proper placing of some specimens collected in Tahiti, I made a preliminary review of the present situation in so far as materials and data were available. The following preliminary notes may be of interest and may assist in attracting attention to the problems presented by the literature and material. I trust that they may later be expanded into a more satisfactory account.

The genus *Microdictyon* was founded by Decaisne (Arch. Mus. Nat., Paris, vol. 2, p. 115, 1841) to receive a plant collected at Djedda on the Arabian coast of the Red Sea by Botta, and to include the *Conferva umbilicata* Velley and the plants later referred to it. Decaisne designated the Red Sea plant *Microdictyon Agardhianum* and considered it distinct from the Mediterranean plant and from that of the Pacific Ocean. In 1842 (Ann. Sci. Nat., Bot., ser. 2, vol. 17, p. 327) he admitted three species to the genus; viz., *M. Agardhianum* D'ne, *M. Velleianum* D'ne, and *M. tenuius* D'ne. Decaisne seems to have deliberately rejected Velley's specific name as being unsuitable, renaming the species "*Microdictyon Velleianum*" but basing his binomial on the specimen of Gaudichaud from Honolulu in the Hawaiian Islands. In 1866, J. E. Gray (Seemann's Jour. of Botany, vol. 4, pp. 66–69 and 291–293) revised the genus, distinguishing six species; viz., *M. Velleyanum* D'ne, *M. calodictyon* D'ne, *M. Montagnei* Harv., *M. Kraussii, M. tenue* Gray, and *M. tenuius* D'ne. Gray's synonymy, however, seems somewhat confused.

Ever since Gray's paper it has been outspokenly or seemingly tacitly assumed that the type of Velley's *Conferva umbilicata* either came from the Hawaiian Islands or was identical with Gaudichaud's specimen collected there. Velley's plants, as is indicated by the title of his paper, came from New South Wales. They were of a "sombre green tint," were ample, close-meshed, and epiphytic. I have not been able to trace the type of Velley but Harvey's Australian Algae, No. 568, evidently from Sydney Harbor ("abundant throughout Port Jackson, and in the Paramatta River," Harvey, Phyc. Austr.,

vol. 1, pl. 50, 1858), is not only a topotype but is also in close agreement with Velley's figure and description. I feel safe in assuming that Harvey's plant from Sydney Harbor represents the true *Microdictyon umbilicatum* (Velley) Zanard.

J. G. Agardh has described, as *M. obscurum*, a plant from New Caledonia, sent to him by J. E. Gray under the name of *Microdictyon calodictyon*. *M. obscurum* has something of the aspect of *M. umbilicatum* (as limited) but has coarser cells throughout.

I have not seen Gaudichaud's plant, referred to by Decaisne as the type of his "*M. Velleianum*," but there seems to be only one species common about Honolulu (the type locality) and that is a very coarse species (cf. Tilden, Amer. Algae, No. 446, *sub M. umbilicatum*) comparable only to the later described *M. crassum* J. Ag. from the Bahama Islands. The Bahama plant, however, has cells nearly half again as large as those of the Oahu specimens. Assuming these topotype Oahu specimens to be the same as those of Gaudichaud's collections, they may be considered to represent the "*M. Velleianum*" of Decaisne as restricted to specimens he had in mind, but disregarding his synonymy.

Another specimen from the Pacific Ocean is represented by No. 89 of Harvey's Friendly Island Algae and was issued by him under the name of "*Microdictyon Montagnei?.*" Reinbold (Siboga Exp., Mon. 59*a*, p. 67, 1913) has shown that Harvey's specimen is provided with definite tenacula, as points of attachment in the anastomoses of the filaments—a character thus far peculiar to it. I have found these tenacula in a *Microdictyon* from Tahiti, doubtless to be referred to the same species. J. E. Gray legalized the combination *M. Montagnei* Harv. in his paper of 1866. There is an earlier binomial, viz., *M. Montagneanum* Endlicher (Gen. Pl., Suppl. III, p. 14, 1843), to be considered. This, however, is not only different in orthography but is clearly a synonym of *M. calodictyon* (Mont.) Kuetz., a distinct species inhabiting the shores of the Canary Islands.

Okamura (Icones Jap. Algae, vol. 2, pp. 105–108, pl. 80, figs. 8–12, 1910) has referred a Japanese specimen to *Microdictyon pseudohapteron* Gepp and Gepp, a species I shall discuss later. While there seems to be a considerable resemblance, Okamura's plant has primary filaments as broad as "410μ," while *M. pseudohapteron*, judging from the illustrations, is a much more delicate species with primary filaments not over one-half the diameter of those of the Japanese plant. I consequently propose the name **Microdictyon Okamurai** for the Japanese plant.

In this connection, I may mention a specimen in Herb. Farlow collected by Charles Wright (No. 71) on the United States North Pacific Exploring Expedition under Commanders Ringgold and Rodgers, 1853–56, which it seems proper to refer also to *M. Okamurai.* On the label of this specimen the locality has been changed from the printed legend, "Bonin Islands,'" to "Sidney." While there is a possibility of the specimen having been collected at Sydney, Australia, in view of the close agreement with the Japanese species described by Okamura, it seems to me most probable that there has been a confusion of labels and that the plant distributed came from Japanese waters, or possibly from Sydney Island in the Phoenix group.

Heydrich has instituted a genus *Rhipidiphyllum* (Hedwigia, vol. 33, p. 281, 1894) to receive a minute plant from Formosa which he has considered identical with *Anadyomena reticulata* Askenasy from Dirk Hartog Island on the northwestern Australian coast, an identification which is uncertain. The status of *Rhipidosiphon* is doubtful and its relation to or identity with *Microdictyon,* not to be determined without a further study of Heydrich's material. Okamura (Illus. Jap. Algae, p. 91, pl. 30, 1902) has referred a fair-sized Japanese plant to this genus and species and has distributed a very satisfactory specimen (Alg. Jap. Exs., No. 98, 1903). Okamura's plant lacks "tenacula" even in the sense indicated by Heydrich (*loc. cit.*, p. 282) and is clearly a species of *Microdictyon* distinct from any described. I doubt its being identical with Askenasy's species and suggest the provisional name of **Microdictyon japonicum** sp. nov. It is related most closely to *M. Palmerii* but the primary filaments have shorter and more slender segments. Yamada (Bot. Mag. Tokyo, vol. 39, p. 83, fig. 2, 1925) has also described a Formosan plant under the name of *Rhipidisiphon nigrescens,* stating that the color is darker and the meshes finer than in *R. reticulatum* (Ask.) Heydrich. Yamada gives no measurements but his figures indicate a true *Microdictyon,* distinct from any described, and I suggest the provisional combination of **Microdictyon nigrescens** (Yamada).

As to *Microdictyon calodictyon* (Mont.) Kuetz. of the Canary Islands, the species might be attributed to Decaisne by implication, but, so far as I know, Kuetzing (Spec. Alg., p. 512) was the first to use the actual binomial. Judging from topotypes which agree with Montagne's plate (in Barker-Webb et Berthelot, Hist. nat. des Isles Canar., vol. 3, pt. 3, pl. 8, fig. 1 *a–c,* 1841), this is a species with delicate filaments, minute openings, meshes at times obsolete, and

abundance of free ends, particularly on the margins. It seems to be a perfectly distinct species although resembling in color and fine mesh both *M. umbilicatum* and *M. obscurum*.

The Mediterranean species, of which I can trace with certainty only one, is a loose and delicate net, with slender filaments, and very large interstices. It seems clearly the *Microdictyon tenuius* (Ag.) D'ne, a quite distinct species.

There seem to be two distinct species of *Microdictyon* in the West Indian region, *M. crassum* J. Ag., of which excellent specimens collected by M. A. Howe have been distributed by the New York Botanical Garden, and an irregular, much more delicate, loose-meshed species, recorded by Boergesen (Mar. Alg. Danish West Indies, pt. 1, p. 26, 1913) as *M. umbilicatum*. The latter does not seem to me to be the Mediterranean *M. tenuius* (Ag.) D'ne, to which it approaches most closely, but differs particularly in less regular frond, finer mesh, uniformly shorter ultimate cells, and slightly broader primary filaments. I propose for it the name of **Microdictyon Boergesenii.**

There are two or three species indicated from the Cape region in South Africa or in the western Indian Ocean. One of these, *Microdictyon pseudohapteron* Gepp and Gepp (Trans. Linn. Soc., ser. 2 (Zool.), vol. 12, pt. 4, p. 375, pl. 47, figs. 1–4, 1909), from Amirante Island, seems to be a slender species, having crenellated attaching membranes to the tips of the branchlets, a feature peculiar to it and to the Japanese plant mentioned previously under the name of *M. Okamurai*. These tips are intermediate between the very simple or slightly annulate adhesions of most other species thus far mentioned and the tenacula of *M. Montagnei* Harv.

J. E. Gray described a species from Natal collected by Krauss as *Microdictyon Kraussii*, and I can find no other reference except that Barton (Jour. Bot., vol. 31, p. 56, 1893) gives "*M. umbilicatum*, Port Natal, Krauss." From Gray's description it seems to be a dark-colored species with very slender filaments.

There is in Herb. Farlow at Harvard University a single specimen of a very delicate species, light-colored, regularly flattened and reticulate, with very slender filaments and small but distinct meshes. It is related to *M. Boergesenii* but is of finer mesh and more regular and delicate structure. I propose the name **Microdictyon Palmerii,** since it appears not to have been described. It was collected at Guadalupe Island off the coast of Mexico by Dr. E. Palmer. It has much longer segments in the primary filaments than has any other species.

There remains for discussion the original species of Decaisne, viz., *M. Agardhianum*. This was collected by Botta at "Djedda" on the Arabian coast of the Red Sea. I am informed by Mr. G. Hamel that there is no such specimen in the Decaisne collection at the Museum at Paris, nor any specimen of *Microdictyon* from the Red Sea in any of their collections. Gray, however, names (*loc. cit.*, pp. 291, 292) a *M. tenue*, from the Red Sea, which he found in Herb. Lenormand, sent by Decaisne to Lenormand in 1841 and inscribed "*M. Agardhianum* Dec." Decaisne evidently considered his species distinct from the Mediterranean plant (*M. tenuius*) and from the Pacific plant. He says that his *M. Agardhianum* is smaller than the one figured by Velley (*M. umbilicatum*) and forms a simple foliaceous expansion, almost flat, from the center of which, however, spring a fairly considerable number of lamellae. Decaisne's *M. Agardhianum* must remain a "*species incerta*" until Red Sea material is available or until the type specimen emerges from its hiding place. It seems to me probable that it is a distinct species.

The species mentioned above may be distinguished tentatively by the characters of the following provisional key based upon only the more obvious differences:

1. Fronds delicate, filaments slender (primary filaments usually not over 200μ diam.) 2
1. Fronds coarse, filaments robust (primary filaments usually 200μ or over) 7
2. Fronds lax, meshes broad 3
2. Fronds compact, meshes fine to minute 4
3. Meshes very large, primary filaments up to 120μ, segments 3 times as long. ..... **M. tenuius**
3. Meshes medium, primary filaments up to 120μ, segments 2–3 times as long. ..... **M. japonicum**
3. Meshes medium, primary filaments up to 160μ diam., segments up to 8–9 times as long ..... **M Palmerii**
3. Meshes medium, primary filaments up to 200μ diam., segments 3–4 times as long ..... **M. Boergesenii**
4. Anastomoses by definite tenacula ..... **M. Montagnei**
4. No tenacula present 5
5. Meshes minute, often closed ..... **M. calodictyon**
5. Meshes small, all open 6
6. Primary filaments up to 170μ ..... **M. nigrescens**
6. Primary filaments up to 200μ ..... **M. umbilicatum**
6. Primary filaments up to 300μ ..... **M. obscurum**
7. Anastomosing membrane distinctly crenellated 8
7. Anastomosing membrane not distinctly crenellated 9
8. Primary filaments about 200μ diam. ..... **M. pseudohapteron**
8. Primary filaments about 400μ diam. ..... **M. Okamurai**
9. Primary filaments about 500μ, ult. segments 180μ ..... **M. Velleyanum**
9. Primary filaments about 650μ, ult. segments 300μ ..... **M. crassum**

SPECIES OF UNCERTAIN POSITION

Microdictyon Agardhianum Decaisne. Djedda, Red Sea, *Botta.*
Microdictyon Kraussii J. E. Gray. Natal, *Krauss.*

SPECIES TO BE REJECTED

Microdictyon spongiola Berth., = *Boodlea?*
Microdictyon Schmitzii Miliar., = *Boodlea?*
Microdictyon clathratum Martens, = *Cystodictyon.*

DIAGNOSES OF NEW SPECIES, ETC.

Microdictyon Palmerii sp. nov.

Frondibus laeteviridibus, plus minusve orbicularibus, plane foliaceis, basi inaequali umbilicata affixisque, usque ad 4 cm. diam., marginibus, irregularibus, sinuatis lobatisve, delicatulis, tenuibus, lacunis parvulis; filamentis primariis radiantibus, opposite et stellate ramosis, segmentis usque ad 160μ diam., usque ad 8–9-plo longioribus; filamentis ultimis usque ad 60μ diam., 2–3-plo longioribus, ovato-lanceoideis usque ad lageniformibus; membranis anastomosantibus planis et inconspicuis; rete irregulari, interstitiis in magnitude variabilibus, plus minusve magnis, segmentis liberis frequentissimis.

Guadalupe Island, off the Pacific Coast of Mexico, collected by Dr. E. Palmer. Type in Herb. Farlow at Harvard University.

Microdictyon Boergesenii sp. nov.

Frondibus laeteviridibus, laxis, irregularibus, cum algis aliis intertextis, usque ad 2 cm. diam., marginibus filamentis curtis liberisque compositis; filamentis primariis usque ad 200μ diam., usque ad 3-plo longioribus, segmentis ultimis 80–100μ diam., usque ad 3-plo longioribus, obtuse conoideis; membranis anastomosantibus planis et inconspicuis; rete irregulari, interstititiis in forma magnitudineque variabilibus, plus minusve magnis; ramificatione plerumque oppositis, numquam (?) stellatis; segmentis liberis omnino frequentissimis.

Dredged in 24 meters, opposite Cruz Bay, St. Jan Island, Virgin Islands, West Indies, Boergesen, No. 1910. Type No. 207386, Herb. Univ. of California.

Microdictyon Okamurai sp. nov.

Described and figured by K. Okamura, Icones of Japanese Algae, vol. 2, pp. 105–108, pl. 80, figs. 8–12, 1910, under the name of *Microdictyon pseudohapteron* Gepp and Gepp, which it resembles; but it is a much coarser plant as may be seen on comparing the figures of Okamura quoted above with those of the Gepps in Jour. Linn. Soc., ser. 2 (Zool.), vol. 12, p. 375, pl. 47, figs. 1–4, 1909. Both the Indian Ocean and the Japanese plants need more study, but we know the primary filaments of *M. Okamurai* measure 410μ in diameter while those of the true *M. pseudohapteron* are probably not more than half as broad.

Microdictyon japonicum sp. nov.

Rhipidisiphon reticulatum Okamura, Illus. Jap. Algae, vol. 1, p. 91, pl. 30, 1902, Alg. Jap. Exs., No. 98, 1903 (neither of Askenasy nor of Heydrich).

Microdictyon nigrescens (Yamada) comb. nov.

Rhipidisiphon nigrescens Yamada, Bot. Mag. Tokyo, vol. 39, p. 83, fig. 2, 1925.

CONTRIBUTIONS TOWARD A KNOWLEDGE OF THE LIFE-HISTORIES OF THE MELANOPHYCEAE

A PRELIMINARY REPORT

BY

MARGRET ESTHER MYERS

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CONTRIBUTIONS TOWARD A KNOWLEDGE OF THE LIFE-HISTORIES OF THE MELANOPHYCEAE

A PRELIMINARY REPORT

BY

MARGRET ESTHER MYERS

Of the sporeling or embryonic stages in the development of the vegetative body of the Melanophyceae but little is known, and that little of only a few members, although the 'post-embryonal' stages have been worked out for a considerable number of species through several groups of this subclass.

Kuetzing (1843) pictured the young thallus of *Laminaria saccharina* on a "protonematischen Bildung." Thuret's (1850) work made known the earliest stages but did not go beyond the first few segmentations of the germinating zoospore or zygote. Thuret (1850), Drew (1910), and Killian (1911) studied members of the Laminariales and pictured the gametophyte with the young sporophyte attached, while Williams (1900, 1912) reported on the protonema-like developmental stages; but all failed to interpret correctly what they observed. Not until Sauvageau and Kylin (1915 and 1916) published their results was any clear indication given of the complexity of these early stages.

The investigations of the writer were begun at the Puget Sound Biological Station in 1924 and have been continued at the University of California. The existence of representatives of most of the natural orders, and the large number of species found on the Pacific Coast, make it a very favorable place in which to carry on a study of these forms. It is my intention therefore to continue the culture experiments in order to test the results secured by other investigators concerning which there appears to be some disagreement, as noted on page 111.

I wish to thank Professor T. C. Frye of the University of Washington, Professor H. Kylin of the University of Lund, Sweden, and Professor W. A. Setchell of the University of California for their interest and assistance in this work. It was under the guidance of Professor Frye and Professor Kylin at the Puget Sound Biological

Station that I made my first successful attempts to raise certain brown algae in culture. Professor Setchell has furnished me with facilities which have made the present work possible, and in addition has given me much valuable assistance and advice.

The present preliminary report is restricted to two Pacific Coast species of the Laminariales, namely *Postelsia palmaeformis* and *Laminaria Sinclairii*, although other species and other orders are also being studied. Only those results are here reported which the progress of the investigation has justified.

The species investigated by Sauvageau were *Saccorhiza bulbosa*, *Laminaria digitata*, *Laminaria saccharina*, and *Alaria esculenta*. Kylin studied *Laminaria digitata* and *Chorda filum*. Following this pioneer work came the work of Kuckuck (1917) on *Laminaria saccharina*. Pascher (1919) worked on the same species, Yendo (1919) worked on *Alaria crassifolia*, Williams (1920–21) on *Laminaria* and *Chorda*, Ikari (1921) on *Laminaria religiosa*, and Printz (1921–22) on *Alaria esculenta* and *Alaria Pylaii*. The only Pacific Coast species as yet reported on is *Macrocystis pyrifera* (Brandt, 1923).

REVIEW OF PREVIOUS WORK

The Laminariales are the most complicated in structure of any of the brown algae, having a definite holdfast, stipe, and blade or blades, while some of them have air bladders to make them float. A complicated system of mucilage canals and secretory cells is present in many of them, with sieve tubes which are very similar to those found in the Spermatophytes. The species are the largest in size of any of the Thallophytes, some of them being equal in length to the height of our highest trees.

So far as is known, the macroscopic plants of the Laminariales have only unilocular organs of fructification, which are presumably zoosporangia. Kylin (1918, p. 36), however, has demonstrated that a reduction of the chromosome number takes place in the first division of the sporangia of *Chorda filum*, which suggests that all the motile spores from these have a haploid number of chromosomes and should grow into gametophytes. This is probably true throughout this family.

It has been established by Sauvageau, Kylin, Yendo, Kuckuck, Pascher, Ikari, Williams, and Printz that in the Laminariales the

gametophytes are microscopic and, so far as known, either strictly or usually dioecious, although the free sperms have been observed by one person only, namely Williams. The gametangia are unilocular instead of plurilocular, as in the case of the simpler browns, although Ikari has noticed paucilocular male gametangia in *Laminaria religiosa*. The gametophyte, according to most reports, appears to be not only microscopic but short-lived. Kuckuck and Pascher found dwarf sporophytes of *Laminaria saccharina* bearing zoospores.

Brandt's results with *Macrocystis pyrifera* do not agree fully with the foregoing, as he found no satisfactory evidence of the presence of male or antheridial plants, and nothing that could be identified as an oogonium or egg cell. The cells from which the embryos developed appeared to be single cells, sometimes one or more additional cells being present.

METHODS

The culture solution used in the present investigation is that recommended by Kylin, and consists of filtered sea water to which has been added traces of calcium phosphate and sodium nitrate. The best results have been obtained with water which has been sterilized in the autoclave at fifteen pounds steam pressure for from ten to fifteen minutes, as the water from San Francisco Bay contains a great deal of organic matter and a corresponding number of bacteria which it is impossible to eliminate successfully by filtering, even through sand.

Pieces of well-washed sori which contain mature zoosporangia are put in dishes of the culture solution and left there overnight. A few are allowed to remain longer, but this is not usually necessary, as the spores are soon discharged and the old pieces of sorus are liable to decay if left too long in the solution. A small amount of the culture solution is added from time to time as evaporation lowers the level of the solution in the culture dishes and they are stirred up about once a week in order to aerate them. The spores of most plants are found to be germinating on the second or third day. The growth at first is rapid, so that within a week there is a brown layer over the bottom and sides of the dish.

The cultures are kept in a cool room with the temperature between 12° C and 16° C, which seems to be very favorable for growth. Those cultures which have been placed in a slightly warmer place usually

develop very poorly and are finally completely destroyed by bacteria. For some time some of the cultures were kept at a temperature as low as 4° C, and it was at this temperature that the first fruiting gametophytes of *Laminaria Sinclairii* were found. The gametophytes of *Postelsia palmaeformis* developed at 4° C, while oogonia and antheridia were first observed about a week after they had been moved from a temperature of 4° C to 12° C.

Postelsia palmaeformis Rupr.

Postelsia palmaeformis belongs to the Laminariales in the Lessoniaceae. It grows on rocky shores where the surf is strong and usually on projecting rocks, so that the breakers dash over it at low tide. The mature sporophyte stands erect and is usually one-half to three-fourths of a meter in height, having the appearance of a small palm tree. It has a massive holdfast of branched hapteres and a terete, hollow, unbranched stipe which is crowned with a cluster of lanceolate, longitudinally furrowed blades. The fruiting area of the fronds is inconspicuous, merely appearing a little darker than ordinarily when the fronds are held up to the light. The first stages of the sporophyte are very similar to those of the other Laminariales. A minute unbranched frond with a short stipe may be found on the rocks in January. When these fronds are about a centimeter long, vein-like streaks become apparent, running longitudinally up the blade. Soon the blade splits along first one, then others, of these lines, and several blades are formed. Meanwhile ridges begin to appear on the little blades and by the time the blades are two centimeters long they begin to have the pleated appearance of the mature *Postelsia* blades.

With the exception of *Macrocystis pyrifera* (Brandt, 1923) *Postelsia palmaeformis* is the first of the Lessoniaceae to pass through its life-cycle in culture. It is very similar to that of the plants observed by Sauvageau, Kylin, Williams, and Printz in the Laminariaceae, Alariaceae, and Chordaceae, and demonstrates that *Postelsia* of this family conforms in general to the observations which have been made concerning the life-histories of members of the Laminariales as a whole.

The zoospores germinate and form male and female gametophytes which bear antheridia and oogonia, respectively. The eggs are discharged from the oogonia, but remain attached to it, fertilization takes place, and the sporophyte develops from the zygote.

The female gametophyte.—On the germination of the spore, the contents of the spore form a tube in the end of which the protoplast rounds up, and from which it is cut off by a cell wall. While this is happening the chloroplast divides several times, then the nucleus divides once, and two new cells are formed with several chloroplasts in each (pl. 8, fig. 1). These cells may continue to divide and form a short, thick filament (pl. 8, fig. 2), which in turn after several months may develop many branches (pl. 9*b*), or they may enlarge greatly and from one or both a somewhat elongated pear-shaped cell may be produced, which is dark colored and contains a great deal of food material (pl. 8, figs. 2 and 4). This is the oogonium. It may be formed as an outgrowth of the first cell at the end of the germination tube, but this is unusual. If a filament of more than two cells is formed, the cells enlarge and any cell, either terminal or intercalary, may become an oogonium by elongating and becoming filled with food; or any cell may divide and form a side branch, the end cell of which becomes the oogonium (pl. 8, figs. 4 and 6).

The cells of the female gametophytes are somewhat isodiametric and measure from 10 to 25μ. Even after the oogonia have formed and the sporophytes have begun to develop, the gametophytes may continue to grow. Some that are in a culture which is over six months old are still growing and developing sporophytes.

The male gametophyte.—The spores which produce the male gametophytes germinate in the same manner as those which produce the female gametophytes. The male gametophytes are soon noticeable because they are so much smaller, the cells measuring 5 to 8μ by 7 to 10μ (pl. 8, fig. 5), while those of the female gametophytes have a diameter ranging from 10 to 25μ. Male gametophytes have not been found containing more than a dozen cells. They branch in a very irregular manner. The end cells and the cells which branch from the side are probably antheridia. They have much smaller chloroplasts than the other cells, the cytoplasm is dense, and they are often found empty after the sperms are freed. The sperms have not yet been observed after they leave the antheridia.

The formation of the zygote and development of the sporophyte.—The contents of the oogonia are discharged through the end, leaving an empty oogonial cell. The oospores cling to the end of the oogonium through which they were discharged. Fertilization probably takes place at this time, but it has not been observed. The fertilized egg begins to divide immediately. The first cell divisions are transverse,

but very soon they occur also in a longitudinal direction, so that a flattened thallus is formed. This is at first one layer of cells thick, but later on it becomes two or three layers thick. In the meantime, while the thallus is developing, at first one and then several of the basal cells of the thallus send out long colorless prolongations which resemble rhizoids, and these, seeking a place of attachment (pl. 8, fig. 7), grow back around the empty oogonium.

Laminaria Sinclairii (Harv.) Farlow

Although several species of the genus *Laminaria* have been raised in cultures and their development observed and reported on, it is interesting to follow the development of another species.

Laminaria Sinclairii differs from most of the other species of *Laminaria* in that it possesses an elongated, slender rhizome which clings to the rocks by branching hapteres and from which the upright fronds arise. The upright portion consists of a long, slender, slightly flattened stipe, an inconspicuous meristematic region, and a long, narrow, expanded blade. It contains mucilage ducts in both the stipe and blade.

The life-history is very similar to that of the other members of the genus *Laminaria* which have been studied.

The female gametophyte.—On germinating, the zoospores of *Laminaria Sinclairii* form the regular dumbbell-like structures. The female gametophytes then develop as short filaments of irregularly shaped cells which may be anywhere from 10 to 20μ wide and from 10 to 100μ long. They are very variable, but the extremes in length usually do not occur until the cultures are several months old. These cells develop protuberances on one side which later are cut off by a cell wall, thus forming side branches. The first cells cut off, or the end cells of some of these branches, may have very dense contents and are evidently the oogonia containing the eggs. The egg is forced out of the oogonium through the tip but remains attached to it (pl. 8, fig. 13). The egg is probably fertilized at this stage, but the process of fertilization has not been observed. The gametophytes continue to grow and produce more oogonia. Some which are eight months old at the time of writing have been reproducing continually for a period of six months and are still doing so.

The male gametophyte.—The first stages of development of the male and female plants are the same. The same dumbbell-like structure is formed, but it is soon noticeable that some of the filaments

which develop are much more slender than others. These belong to the male plants. The filaments of these are from 5 to 8μ in diameter and the cells of the filaments from 7 to 15μ in length. The cells are not so irregular and swollen as in the female gametophytes. They form slender, irregularly branched filaments. The end cells of these filaments or of their branches may become antheridia, or antheridia may develop as one-celled outgrowths from the sides of the branching filaments (pl. 8, figs. 8, 9). The chloroplasts cannot be distinguished in them so clearly as in the other cells and they are filled with rather dense cytoplasm. Later they are found empty. The male gametophytes also continue to grow after fruiting.

The young sporophyte.—The fertilized eggs begin to develop at once. The first divisions are in a transverse direction so that the young sporophyte is at first a row of rather flattened cells. Then division takes place longitudinally and a broad flattened structure is formed, which at first is one layer of cells thick. Meanwhile from the end nearest the oogonium, rhizoids develop and grow back around the empty oogonium (pl. 8, figs. 11, 12, 13).

Further development of the gametophyte.—Even after the young sporophytes are formed, the gametophytes continue to grow; at the time of writing this, some of them are eight months old. They form a dense silt-like brown mat on the bottom of the culture dish. They continue to produce new oogonia and antheridia, and in the cultures at the present time all stages may be found from the oogonium to six-months-old sporophytes. The oldest sporophytes are still microscopic and surrounded by dense mats of gametophyte filaments. The male and female gametophytes in these old cultures may easily be distinguished from one another by the diameter of the filaments, the male being much smaller. The male filaments also are usually longer than those of the female.

In cultures both of *Laminaria Sinclairii* and *Postelsia palmaeformis,* the gametophytes have continued to persist even after the sporophytes are formed. The male gametophytes of *Postelsia* are very small and difficult of detection in the culture and the gametophytes as a whole do not form such dense mats as are found in the cultures of *Laminaria Sinclairii.* The gametophytes of *Laminaria Sinclairii* are so vigorous and form such conspicuous mats of filaments that they may have been observed in nature if they grow as well outside as they do in cultures. They would probably not be described, as so far no method of reproduction such as is usually

looked for on the filamentous forms of Melanophyceae has been observed. They are still growing vigorously, however, so it is not yet evident how long they are able to survive, or into what form or forms they may ultimately develop. The prolonged growth may possibly be due to culture conditions, especially those of continued low temperature, which may not occur in nature, but it seems possible that conditions may be more favorable for continued growth in their natural habitat than they are in the culture dish. Ikari has noted that the development of the young sporophyte is affected very definitely by temperature.

SUMMARY

Postelsia palmaeformis of the Lessonieae of the Lessoniaceae has been observed to have a microscopic gametophyte form similar to those observed for members of the Laminariaceae, Alariaceae, and Chordaceae, and the same type of alternation of generation.

Although Brandt did not find satisfactory evidence of male plants and of oogonia in *Macrocystis pyrifera,* which is also one of the Lessoniaceae, they are very easily recognized in cultures of *Postelsia palmaeformis,* which would lead one to look for them in other genera of the same family.

The microscopic male and female gametophytes, and the formation of young sporophytes of *Laminaria Sinclairii,* have been studied in culture, and the results confirm in one more case what is expected to be true of all the members of the Laminariaceae.

The gametophytes of both *Laminaria Sinclairii* and *Postelsia palmaeformis* continue to grow even after they have first produced gametes, and continue to produce gametes for at least as long as six months. They are still under observation at the time of writing and are still producing gametes.

The gametophytes of *Laminaria Sinclairii* contain many more cells and are much more vigorous under the conditions in which they have been observed than are those of *Postelsia palmaeformis.* This may be due to the culture methods being more favorable to *Laminaria Sinclairii* or it may be due to innate differences in the plants themselves. If the latter is true, there is still the question whether it applies to Lessoniaceae and Laminariaceae as a whole or whether the species in each group vary.

The male and female gametophytes of both plants after the first few weeks are easily distinguished from one another by their size, although when the spores first germinate it is impossible to tell which of the plants are male and which are female.

So far I have found no evidence of the young sporophytes of either *Laminaria Sinclairii* or *Postelsia palmaeformis* producing zoospores, as reported for *Laminaria saccharina* by Kuckuck and Pascher.

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EXPLANATION OF PLATES

PLATE 8

(All the figures of Plate 8 are camera lucida drawings, × 340.)

Postelsia palmaeformis Rupr.

Fig. 1. Empty spore with two-celled female gametophyte attached.

Fig. 2. Female gametophyte, with two young oogonia forming.

Fig. 3. Two-celled female gametophyte, with empty oogonium and young sporophyte above.

Fig. 4. Female gametophyte with two mature and one young oogonia.

Fig. 5. Male gametophyte with antheridia.

Fig. 6. Female gametophyte with four empty oogonia and one young sporophyte.

Fig. 7. Young sporophyte.

Laminaria Sinclairii (Harv.) Farlow

Fig. 8. Young gametophytes.

Fig. 9. Male gametophyte with antheridia.

Fig. 10. Male gametophyte with antheridia.

Fig. 11. Female gametophyte with one empty oogonium and one young sporophyte attached.

Fig. 12. Female gametophyte.

Fig. 13. Empty oogonium and oospore.

Fig. 14. Female gametophyte with three empty oogonia and three young sporophytes.

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PLATE 9

a. Photomicrograph of *Laminaria Sinclairii,* × 102, showing young sporophytes and male and female gametophytes. This picture was taken of material from an eight months old culture.

b. Photomicrograph of *Postelsia palmaeformis,* × 671. Taken from an eight-months old culture. Female gametophyte with some elongated pear-shaped oogonia.

a

b

NEW SPECIES OF PLANTS FROM INDO-CHINA. II.

BY

ELMER D. MERRILL

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NEW SPECIES OF PLANTS FROM INDO-CHINA. II

BY

ELMER D. MERRILL

The first paper[1] of this series was published in October, 1924, and the present one, like its predecessor, has been based on material collected and submitted to me for study by Dr. A. Petelot. In it eighteen species are described as new, while eighteen others previously described are recorded from Indo-China for the first time. No representatives of the genera *Muhlenbergia, Pseudotrophis, Nasturtium, Sedum, Trifolium, Geranium, Aucuba,* and *Crawfurdia* have hitherto been recorded from Indo-China. The material on which this paper is based is deposited in the herbarium of the University of California.

GRAMINEAE

Miscanthus Andersson

Miscanthus nepalensis Hack. *in* D.C. Monog. Phan., vol. 6, p. 104, 1889.

Indo-China, Tonkin, Chapa, *A. Petelot 1745,* leg. *Mlle. Colani* November, 1924, det. A. S. Hitchcock. Mountains of northern India to Szechuan Province, China, and Lappas Island. The third species of the genus to be found in Indo-China.

Muhlenbergia Schreber

Muhlenbergia Huegelii Trin. *in* Mém. Acad. Pétersb., ser. 6, vol. 6[2], p. 293, 1845.

Indo-China, Tonkin, Chapa, *A. Petelot 1491,* July, 1924. Himalayan region to Tibet, China, Japan, and Java. The genus is new to Indo-China.

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[1] Univ. Calif. Publ. Bot. vol. 10, pp. 423–430. 1924.

Polypogon Desfontaine

Polypogon lutosus (Poir.) Hitchc. *in* U. S. Dept. Agr. Bull. 772, p. 138. 1920.

Agrostis lutosa Poir, *in* Lam. Encycl. Suppl., vol. 1, p. 249, 1810.

Indo-China, Tonkin, Chapa, *A. Petelot 1796* (det. Hitchcock), April, 1925.

Originally described from Europe: widely distributed in temperate and tropical regions. The second species of the genus to be found in Indo-China. It is more commonly known as *Polypogon littoralis* Sm.

CYPERACEAE

Scirpus Linnaeus

Scirpus ternatanus Reinw. *ex* Miq. Fl. Ind. Bat., vol. 3, p. 307, 1856.

Scirpus chinensis Munro (1857).

Indo-China, Tonkin, Chapa, *A. Petelot 1625,* July, 1924. New to Indo-China. India to China and the Riu Kiu Islands, through the Philippines to Celebes and the Moluccas.

SAURURACEAE

Saururus Linnaeus

Saururus Cavaleriei Lévl. *in* Fedde Repert., vol. 10, p. 149, 1911.

Gymnotheca chinensis Decne. *in* Ann. Sci. Nat., ser. 3, vol. 3, p. 100, pl. 5, 1845; Hook. Ic., vol. 19, pl. 1873, 1889, non *Saururus chinensis* Baill.

Indo-China, Tonkin, Province of Bac Giang, Lang Met, *A. Petelot 1824,* leg. *Mlle. Colani,* May, 1924.

Gymnotheca, a monotypic genus described by Decaisne, was retained by Bentham and Hooker, but in the Natürlichen Pflanzenfamilien it is reduced to *Saururus.* Decaisne's specific name is invalidated in *Saururus,* but no new one appears to be necessary inasmuch as *Saururus Cavalerieri* Lévl. is undoubtedly the same species in spite of Léviellé's short and imperfect description; his type was from Kweichau Province, China. The species (or genus if *Gymnotheca* be retained) is new to Indo-China.

MORACEAE

Ficus Linnaeus

Ficus cardiophylla sp. nov. § *Urostigma.*

Arbor glaberrima, ramis ramulisque teretibus, in siccitate purpureo-brunneis vel rubro-purpureis, leviter lenticellatis, ramulis 1 ad 2 mm. diametro; foliis alternis, chartaceis, in siccitate viridibus, nitidis, levibus, ovatis, integris, perspicue acute acuminatis, basi 3-nerviis, late rotundatis, distincte cordatis, 5 ad 9 cm. longis, 3 ad 6 cm. latis, nervis primariis utrinque circiter 7, patulis, tenuibus, distinctis; petiolo haud articulato, 2 ad 2.5 cm. longo; receptaculis axillaribus, sessilibus, levibus, maculatis, solitariis vel binis, globosis, glabris, 5 ad 7 mm. diametro, pericarpio tenui, bracteis 3, tenuibus, orbicularibus ad subreniformibus, circiter 2 mm. diametro; floribus ♂?, ♀ fertilibus sessilibus vel pedicellatis, circiter 2 mm. longis, perianthi segmentis 1 mm. longis.

Indo-China, Tonkin, Cho Ganh, *A. Petelot 1291,* November, 1923.

Although I have not detected any male flowers in the material available, I am definitely of the opinion that this species belongs in the section *Urostigma,* in the general alliance with *Ficus religiosa* Linn. and *F. Rumphii* Blume, from both of which it is at once distinguished by its smaller, less acuminate leaves, and smaller receptacles.

Ficus Petelotii sp. nov. § *Eusyce?*

Frutex erectus, ramulis parcissime pubescentibus exceptis glaber, ramis ramulisque brunneo-purpureis, haud lenticellatis, ramulis circiter 3 mm. diametro; foliis numerosis, alternis vel subobpositis, oblanceolatis, coriaceis, rigidis, integris, in siccitate brunneis, 7 ad 12 cm. longis, 1.5 ad 2 cm. latis, acuminatis, deorsum angustatis, basi acutis vel abrupte obtusis, supra levibus, puncticulatis, nervis primariis utrinque circiter 15, subtus perspicuis, prope marginem arcuato-anastomosantibus, reticulis laxis; petiolo circiter 1 cm. longo; receptaculis axillaribus, solitariis, pedunculatis, circiter 1.5 cm. longis, 1 ad 1.3 cm. diametro, longitudinaliter circiter 15-costatis, levibus, glabris, obtusis, basi acutis; pedunculo circiter 10 mm. longo, ad apicem 3-bracteato, bracteis late ovatis ad ovato-reniformibus, vix 1 mm. longis; floribus ♂?, ♀ numerosissimis, perianthi segmentis linearilanceolatis, 2 mm. longis, purpureis, ovario subsellipsoideo, 0.6 mm. longo.

Indo-China, Tonkin, Cho Kanh, *A. Petelot 1285,* January, 1923.

The alliance of this species is not clear to me, and in the absence of staminate flowers (at least I have been unable to detect any in the receptacles examined), its section is uncertain, although it probably

belongs in *Eusyce*. It is a stenophyllous erect shrub growing along the margins of small streams, the basal part of the trunk in the specimen available being about 1 cm. in diameter. It is particularly characterized by its oblanceolate, entire, rigid leaves which are conspicuously puncticulate beneath, and by its peduncled, longitudinally ribbed receptacles.

Pseudotrophis Warburg

Pseudotrophis mindanaensis Warb. *in* Perk. Frag. Fl. Philip., p. 165. 1905.

Indo-China, Tonkin, Province of Bac-Giang, *A. Petelot 1962*, leg. *Mlle. Colani*, March, 1925.

The genus as at present constituted is represented by two known species, one occurring in the Key Islands, the present one being known from the islands of Cebu, Leyte, Basilan, and Mindanao in the Philippine Archipelago. The Tonkin specimen is a staminate one and so far as I can determine by a critical comparison with Philippine material presents no characters by which it can be distinguished, even as a variety.

LORANTHACEAE

Elytranthe G. Don

Elytranthe Petelotii sp. nov.

Frutex parasiticus, inflorescentiis exceptis glaber; ramulis teretibus, 3 ad 4 mm. diametro, in siccitate rugosis, leviter lenticellatis; foliis oppositis, coriaceis, rigidis, plerumque plus minusve falcatis, oblongo-lanceolatis ad oblongo-ovatis, acuminatis, basi acutis ad subrotundatis, leviter inaequilateralibus, circiter 15 cm. longis et 5.5 cm. latis, verruculosis, pallide olivaceis, nervis primariis utrinque circiter 15, obscuris; petiolo 2 ad 2.5 cm. longo; inflorescentiis axillaribus, fasciculatis vel solitariis, rhachibus crassis, vix 1 cm. longis, furfuraceis, bifloris, basi bracteis brevibus latissime ovatis instructis; floribus sessilibus, rubris, curvatis, 6.5 ad 7 cm. longis; bracteis coriaceis, late ovatis, obtusis, ferrugineo-furfuraceis, circiter 8 mm. longis; bracteolis binis, quam bracteis majoribus, ad 11 mm. longis, valde imbricatis; calycibus glabris, truncatis, sessilibus, cylindrico-cupulatis, circiter 6 mm. longis; corollae tubo 3.5 ad 4 cm. longo, crasso, curvato, sursum ampliato et 3.5 mm. diametro, glabro, lobis 6, circiter 2.5 cm. longis, partibus reflexis 1.5 cm. longis et 2 mm. latis; staminibus 6, filamentis erectis, 1 cm. longis, antheris linearibus, continuis, 4 ad 5 mm. longis.

Indo-China, Tonkin, Tran Ninh, *A. Petelot 1533,* April, 1924, common on various species of trees, especially on *Quercus.*

A species remarkable in *Elytranthe* by its large bracts and by its even larger bracteoles, the latter being free but strongly imbricate, and like the bracts densely ferruginous-furfuraceous except in the protected parts, which are glabrous. The entire plant is glabrous except the short rachises of the inflorescences, the bracts, and the bracteoles. The 2-flowered rachises are solitary or fascicled in the leaf axils. The species is not closely allied to any of the other known forms from Indo-China.

MAGNOLIACEAE

Illicium Linnaeus

Illicium micranthum Dunn *in* Hook. Ic., vol. 28, pl. *2714,* 1901.

Indo-China, Tonkin, Chapa, *A. Petelot 1776,* April, 1925.

The third species of the genus to be recorded from Indo-China, the specimen cited agreeing closely with the description and figure of Dunn's species. Previously known only from Yunnan Province, China.

ANONACEAE

Polyalthia Blume

Polyalthia Petelotii sp. nov. § *Monoon.*

Frutex vel arbor parva, ramulis junioribus floribusque exceptis glabra; ramis teretibus, glabris, ramulis tenuibus, junioribus breviter adpresse ferrugineo-pubescentibus; foliis chartaceis, oblongis ad oblongo-oblanceolatis, 10 ad 15 cm. longis, 2.5 ad 4 cm. latis, in siccitate pallide olivaceis, nitidis, glabris vel subtus parcissime pubescentibus, basi acutis, apice obtuse acuminatis, nervis primariis utrinque circiter 12, distantibus, tenuibus, arcuato-anastomosantibus, reticulis laxis; petiole 5 ad 7 mm. longo; floribus oppositifoliis, circiter 3.5 cm. diametro, pedicellis 10 ad 12 cm. longis, adpresse ferrugineo-pubescentibus; sepalis subcoriaceis, late ovatis, circiter 13 mm. longis et 10 mm. latis, rotundatis ad late acutis, extus leviter pubescentibus; petalis oblongo-obovatis ad ellipticis, subcoriaceis, 2 ad 2.3 cm. longis, 1 ad 1.5 cm. latis, obtusis ad late acutis, extus adpresse ferrugineo-pubescentibus; staminibus numerosissimis, circiter 2.8 mm. longis; carpellis numerosis, breviter stipitatis, adpresse pubescentibus, cum stylis circiter 3 mm. longis, stylis crassis, cylindraceis, glabris, circiter 1 mm. longis, stigmate glabro, truncato; ovulis solitariis.

Indo-China, Tonkin, Chapa, *A. Petelot 1780*, April, 1925.

Among the described species from Indo-China, this form is probably nearest to *Polyalthia modesta* Finet et Gagnep., from which it differs in its very much larger sepals and petals. The stigmas are entirely glabrous and not at all capitate, being truncate and no thicker than are the cylindric, glabrous, rather stout styles.

HERNANDIACEAE

Illigera Blume

Illigera cucullata sp. nov. § *Appendiculatae.*

Frutex scandens inflorescentiis exceptis glaber, ramulis in siccitate nigricantibus; foliis 3-foliolatis, petiolo usque ad 11 cm. longo, petiolulis 2.5 ad 3 cm. longis; foliolis subcoriaceis, olivaceis, nitidis, 8 ad 13 cm. longis, 5 ad 10 cm. longis, late ellipticis ad late elliptico-ovatis, apice breviter abrupteque acuminatis, basi plerumque leviter inaequilateralibus, late rotundatis, axillis subtus haud barbatis, nervis utrinque circiter 5, distinctis; cymis amplis, pedunculatis, pedunculo 5 ad 7 cm. longo, multifloris, axillaribus usque ad 12 cm. longis, terminalibus multo longioribus, partibus junioribus dense subferrugineo-pubescentibus, bracteolis parvis, ovatis ad oblongo-ovatis; floribus circiter 1.4 cm. longis, calycis tubo dense pubescente, sepalis oblongis, acutis, leviter pubescentibus, 12 ad 14 mm. longis, 3 ad 3.5 cm. latis; petalis lanceolatis ad oblanceolatis, acutis, leviter pubescentibus, acutis, deorsum, angustatis, 11 mm. longis; filamentis leviter pubescentibus, 9 mm. longis; stylis 8 mm. longis, leviter pubescentibus, stigmate flabellato, undulato, 2.5 mm. diametro; nectariis staminalibus magnis, stipitatis, basi cucullatis, sursum planis, 4 mm. longis, membranaceis, apice obtusis, leviter erosis, stipite 1 mm. longo; fructibus 3 ad 3.3 cm. longis, bialatis, alis aequalibus, coriaceis, in siccitate castaneis, nitidis, glabris, late suborbiculari-rotundatis, 4 ad 5 cm. diametro.

Indo-China, Tonkin, Chapa, *A Petelot 1646* (flower), July, 1924, *1792* (fruit), April, 1925. Local name *giay gam.*

A species well characterized by its entirely glabrous leaves, its unusually large flowers, its broadly 2-winged fruits, the fruits otherwise obscurely carinate; and especially by its large, cucullate, stipitate, petaloid staminodes or staminal nectaries. In its large flowers it approaches *Illigera rhodantha* Hance but is otherwise not closely allied to that species.

CRUCIFERAE

Nasturtium R. Brown

Nasturtium officinale R. Br. *in* Ait. Hort. Kew., ed. 2, vol. 4, p. 110, 1812.

Indo-China, Tonkin, Chapa, *A. Petelot 1805,* April, 1926. Common water cress, now in most temperate regions, perhaps introduced here, but at any rate not previously recorded from Indo-China.

CRASSULACEAE

Sedum Linnaeus

Sedum lineare Thunb. Fl. Jap., p. 187, 1784.

Indo-China, Tonkin, Chapa, *A. Petelot 1382,* July, 1924. The identification is by Mr. Lloyd Praeger, who states that the specimen agrees with Thunberg's species. Japan, Riu Kiu Archipelago, China. The genus is new to Indo-China.

POLYGALACEAE

Polygala Linnaeus

Polygala lancilimba sp. nov. § *Chamaebuxus.*

Suffrutex erectus, ramosus, e radicibus incrassatus, partibus junioribus leviter pubescentibus, caulibus circiter 3 mm. diametro, ramulis tenuibus, 1 ad 1.5 mm. diametro; foliis lanceolatis, chartaceis, olivaceis, subtus pallidioribus, glabris, integris, tenuiter acuminatis, basi acutis, 5 ad 10 cm. longis, 8 ad 15 mm. latis, nervis lateralibus utrinque circiter 5, tenuibus, indistinctis, saepe obsoletis vel subobsoletis; petiolo 5 ad 12 mm. longo; racemis terminalibus, simplicibus, usque ad 14 cm. longis, paucifloris, leviter pubescentibus, erectis; floribus 1.8 ad 2 cm. longis, glaberrimis; bracteis lanceolatis, acuminatis, circiter 5 mm. longis, pedicellis subaequantibus; sepalis exterioribus inaequalibus, superioribus, cucuelato-navicularibus, 7 mm. longis, aliis oblongo-ellipticis, obtusis, concavis, 4.5 mm. longis, 1.5 mm. latis, alis oblongo-obovatis, rotundatis, deorsum angustatis, 1.5 cm. longis, 7 mm. latis; corolla 1.8 ad 2 cm. longa, carinae crista 2-vel 3-lobulata, lobulis 0.8 ad 1.2 mm. longis, oblongis, obtusis; ovario compresso, glabro; capsulis suborbicularis, 8 mm. diametro, compressis, perspicue retusis, bialatis, alis superne 1.5 mm. latis; sepalis caducis, disco annulari, integro.

Indo-China, Tonkin, Chapa, *A. Petelot 1769*, April, 1925.

A species not closely allied to any of the forms previously recorded from Indo-China, nor can I refer it to any of the Chinese or Siamese species after critically examining the various descriptions. It is well characterized by its habit; its lanceolate, glabrous, obscurely nerved leaves; and the few-lobed crests, the first lobe being nearly free, the other two more or less united. The crest is but about 2 mm. wide and is less than 1.5 mm. high. There are two other species of this genus represented in Petelot's collection that differ from any of the recorded species of Indo-China, but the material in each case is imperfect. *No. 1809* from Chapa, fruiting specimen, undoubtedly represents an undescribed species, while the same may be true in reference to *No. 1694*, an undershrub from Mau-Son, Tonkin, the specimen with immature flowers.

SAXIFRAGACEAE

Itea Linnaeus

Itea indochinensis sp. nov.

Arbor parva, ramulis et subtus foliis et inflorescentiis molliter villosis, ramis teretibus, glabris; foliis ellipticis ad oblongo-ellipticis, subcoriaceis, 10 ad 15 cm. longis, 4.5 ad 8 cm. latis, supra glabris vel junioribus ad costa nervisque puberulis, olivaceis, nitidis, subtus pallidioribus, molliter villosis, basi obtusis ad late acutis, apice acuminatis, margine serrulatis, nervis primariis utrinque 8 ad 11, curvato-adscendentibus, perspicuis; petiolo 1 ad 1.5 cm. longo; racemis axillaribus, plerumque fasciculatis, densis, 5 ad 7 cm. longis, circiter 1 cm. diametro, villosis; pedicellis circiter 2 mm. longis; sepalis lanceolatis, acuminatis, 1.2 ad 1.5 mm. longis; petalis oblongis, obtusis, erectis, haud recurvatis, 2.5 ad 2.8 mm. longis; filamentis leviter pubescentibus, 3 ad 3.5 mm. longis, ovario leviter villoso.

Indo-China, *A. Petelot 1687* (type), a form of the same species probably represented by *Petelot 1024* from Phu Ho, but with somewhat less pubescent leaves and longer more slender racemes which attain a length of 7 cm.

The species is well characterized by its pubescent leaves and may, in part, have been included by Gagnepain in his conception of *Itea chinensis* Hook. et Arn. as described in Leconte, Fl. Gén. Indo-Chine, vol. 2, p. 686, 1820. It is at once distinguished from the latter species not only by its indumentum but also by its more numerously nerved leaves, typical *Itea chinensis* Hook. et Arn. having smaller glabrous leaves with but five pairs of lateral nerves.

ROSACEAE

Pyrus Linnaeus

Pyrus Calleryana Decne. Jard. Fruit, vol. 1, pl. 8, 1872.

Indo-China, Tonkin, Chapa, *A. Petelot 1784,* April, 1925, with the local name *cay moc cop.* New to Indo-China, but probably planted here. Widely distributed in China, often cultivated. The sand pear.

LEGUMINOSAE

Trifolium Linnaeus

Trifolium repens Linn. Sp. Pl., p. 767, 1753.

Indo-China, Tonkin, Chapa, *A. Petelot 1806,* April, 1925. The genus is new to Indo-China, the species probably introduced. Common white clover, now widely distributed in most temperate regions.

LINACEAE

Ixonanthes Jack

Ixonanthes parvifolia sp. nov.

Frutex glaber, ramis ramulisque teretibus, ramulis tenuibus, 1.5 ad 2 mm. diametro; foliis ellipticis ad obovatis, subcoriaceis, 2.5 ad 5 cm. longis, 1.5 ad 2.5 cm. latis, olivaceis, nitidis, apice rotundatis vel interdum retusis, nervis primariis utrinque circiter 5, distinctis, anastomosantibus, reticulis laxis; petiolo circiter 5 mm. longo; fructibus circiter 12 mm. longis et 8 mm. diametro, valvis lanceolatis, acuminatis; sepalis persistentibus oblongo-ellipticis, obtusis, circiter 6 mm. longis, exterioribus paullo brevioribus.

Indo-China, Tonkin, Cho Kanh, *A. Petelot 2001,* November, 1923, on limestone hillocks, a shrub about 1 m. in height.

A species readily distinguishable among its congeners by its unusually small leaves.

GERANIACEAE

Geranium Linnaeus

Geranium nepalense Sweet, Geran., vol. 1, pl. 12, 1820–22; Knuth, Pflanzenreich, vol. 53, p. 192, 1912.

Indo-China, Tonkin, Chapa, *A. Petelot 1810*, April, 1925. Afghanistan to Ceylon, China, and Japan. No representative of the family has previously been recorded from Indo-China.

VITACEAE

Tetrastigma Planchon

Tetrastigma obtectum (Wall.) Planch. *in* DC. Monog. Phan., vol. 5, p. 434, 1887; Gagnep. *in* Not. Syst., vol. 1, p. 323, 1910.

Vitis obtecta Wall. Cat. no. 6026, 1831–32, *nomen;* Laws *in* Hook. f. Fl. Brit. Ind., vol. 1, p. 657, 1875.

Indo-China, Tonkin, Chapa, *A. Petelot 1789*, April, 1925. This is apparently a small-leaved form of the typical plant, very closely matching *Rock 4067* from Yunnan. Kumaon to Nepaul in India, and rather widely distributed in western China, but hitherto unknown from Indo-China.

THEACEAE

Eurya Thunberg

Eurya stenophylla Merr. *in* Philip. Jour. Sci., vol. 21, p. 502, 1922.

Indo-China, Tonkin, Chapa, *A. Petelot 1802*, April, 1925. The cited specimen differs from the type in its somewhat smaller fruits, which are, however, immature. I do not think that this narrow leaved form can, with propriety, be referred to the polymorphous *Eurya acuminata* DC., nor to the equally polymorphous *Eurya japonica* Thunb., the only two species credited to Indo-China. If the presence or absence of indumentum on the ultimate branchlets be of any value in distinguishing between these two polymorphic species, then *Eurya stenophylla* Merr. is nearer the latter species, as it is entirely glabrous in all its parts. The type of the species was from Kwantung Province, China.

GUTTIFERAE

Hypericum Linnaeus

Hypericum ascyron Linn. Sp. Pl., p. 783, 1753.

Indo-China, Tonkin, Chapa, *A. Petelot 1642*, July, 1924. Widely distributed in China, extending westward to Dahuria. New to Indo-China.

MALASTOMATACEAE

Anerincleistus Korthals

Anerincleistus Petelotii sp. nov.

Frutex erectus, 1.5 ad 2 mm. altus, ramulis et subtus foliis minute brunneo-puberulis, ramis teretibus, glabris, ramulis 1 ad 1.5 mm. diametro, 4-angulatis; foliis oppositis, aequalibus, chartaceis, in siccitate atro-olivaceis, fragilis, subtus pallidioribus, oblongo-ellipticis, 6 ad 9 cm. longis, 2.5 ad 3.8 cm. latis, supra glabris, subtus praesertim ad nervis plus minusve puberulis, minute aureo-glandulosis, margine calloso-denticulatis, apice perspicue acuminatis, basi acutis, 7-nerviis, nervis et nervulis transversalibus numerosis perspicuis; petiolo 1 ad 1.5 cm. longo; floribus axillaribus, fasciculatis vel depauperato-cymosis, 4-meris, pedicellis circiter 7 mm. longis, puberulis; calycis tubo subcylindrico, 4 ad 5 mm. longo, glabro, lobis ovatis, acutis, 4 mm. longis, patulis vel reflexis, integris vel obscure denticulatis; petalis 4, late ovatis, acuminatis, 3 ad 4 mm. longis; staminibus 8, aequalibus, filamentis 1 mm. longis, antheris lanceolatis, 3.5 ad 4 mm. longis, connectivo basi non producto, antice inappendiculato, postice calcarato, appendicibus crassis, obtusis, 0.5 mm. longis.

Indo-China, Tonkin, Chapa, *A. Petelot 1384*, July, 1924, flowers red.

Among the described species of this genus nearest to *Anerincleistus blastifolius* Guillaumin of Annam, differing markedly in its smaller leaves which are minutely glandular beneath, and 7-nerved, not 5-plinerved at the base, the margins calloso-denticulate, not entire, as well as in its large calyx lobes which are at least one-half as long as the calyx tube.

Medinilla Gaudichaud

Medinilla Petelotii sp. nov.

Frutex glaber, ramis teretibus, valde rugosis, ramulis 4-angulatis, et anguste 4-alatis, alis crassis, undulatis; foliis oppositis, aequalibus, chartaceis ad subcoriaceis, oblongo-obovatis, 15 ad 20 cm. longis, 5 ad 8 cm. latis, apice breviter abrupteque acuminatis, basi acutis, perspicue 3-plinerviis vel obscure 5-plinerviis, nervis transversalibus obsoletis

vel valde obscuris; petiolo 1 ad 1.5 cm. longo; inflorescentiis lateralibus, laxe racemoso-paniculatis, pauciflоris, ad nodis in ramis vetustioribus fasciculatis, 5 ad 6 cm. longis; floribus ignotis, pedicellis gracilis, 2.5 ad 3.5 cm. longis; calycibus urceolatis, 1.2 ad 1.5 cm. longis, ovario ut videtur 4 loculari.

Indo-China, Tonkin, Chapa, *A. Petelot 1791,* April, 1925.

Probably belonging in the general group with *Medinilla venusta* King of the Malay Peninsula, but with petioled leaves, and 4-angled branchlets, the flowers not umbellate but racemose-panicled. It is remote from any of the described forms known from Indo-China. The inner pair of nerves are much more prominent than are the outer marginal pair and extend to the apex of the leaf.

CORNACEAE

Aucuba Thunberg

Aucuba chinensis Benth. Fl. Hongk., p. 138, 1861.

Indo-China, Tonkin, Mau Son, *Petelot 1748,* January, 1925. Szechuan and Yunnan to Kwantung Province in China, and Formosa. The genus is new to Indo-China.

ERICACEAE

Vaccinium Linnaeus

Vaccinium Petelotii sp. nov.

Frutex vel arbor glabra, ramulis teretibus vel subteretibus, 2.5 ad 4 mm. diametro, leviter lenticellatis; foliis crasse coriaceis, integris, oblongis ad late oblongo-lanceolatis, 18 ad 21 cm. longis, 4 ad 6 cm. latis, apice longe tenuiter caudato-acuminatis, deorsum angustatis, basi circiter 1.5 cm. latis, subabrupte rotundatis vel subcordato-rotundatis, supra pallide olivaceis, subtus flavido-brunneis, punctatis, nervis primariis utrinque circiter 8, adscendentibus, anastomosantibus, perspicuis, reticulis laxis; petiolo crasso, circiter 4 mm. longo; racemis axillaribus, circiter 5 cm. longis, solitariis, laxis; fructibus ovoideis vel subglobosis, longe (circiter 2 cm.) pedicellatis, glabris, 5 ad 6 mm. diametro, sepalis persistentibus oblongo-ovatis vel oblongo-lanceolatis, acuminatis, circiter 2.5 mm. longis.

Indo-China, Tonkin, Chapa, *A. Petelot 1772,* April, 1925.

A species manifestly belonging in the group with *Vaccinium Dunalianum* Wight which extends from India to Yunnan, differing in its much larger, more numerously nerved leaves which are abruptly contracted and rounded-cordate at the base, not cuneate.

MYRSINACEAE

Ardisia Swartz

Ardisia crispipila sp. nov. § *Akosmos.*

Frutex circiter 3 m. altus, ramulis et petiolis et inflorescentiis densissime crispatulo-villosis, indumento castaneo ad subferrugineo, ramis teretibus, glabris; foliis alternis, integris, chartaceis ad subcoriaceis, oblongo-oblanceolatis, 8 ad 13 cm. longis, 2.5 ad 4.5 cm. latis, apice acuminatis, basi acutis, supra subolivaceis, plus minusve villosis, subtus molliter villosis, utrinque glandulis multis perspicuis instructis; nervis primariis utrinque circiter 20, tenuibus, distinctis, petiolo circiter 1 cm. longo; inflorescentiis axillaribus, solitariis, pedunculatis, stricte racemosis, 8 ad 10 cm. longis; floribus circiter 1.4 cm. diametro; pedicellis dense villosis, 1.5 ad 2 cm. longis; sepalis oblongo-ovatis, acutis, densissime villosis, punctatis, 3 mm. longis, haud imbricatis, ante anthesin apertis; petalis oblongo-ovatis acuminatis, 7 mm. longis, perspicue glandulosis, glabris; antheris ovato-lanceolatis, acuminatis, 4.5 mm. longis, connectivo perspicue glanduloso.

Indo-China, Tonkin, Phu Ho, *A. Petelot 1861,* leg. *Du Pasquier,* January, 1925.

A species, from its general appearance, that might well be placed in the section *Tinus,* but the sepals are not at all imbricate even before anthesis. It is characterized by its soft, dense indumentum which is castaneous to ferrugineous and composed of more or less crisped hairs. In its strictly racemose inflorescences, the flowers being borne along the upper 2 to 4 cm. of the rachis, it differs from most species both of the sections *Akosmos* and *Tinus.* If properly placed in *Akosmos,* it belongs in the general group with *Ardisia Moonii* Clarke, although remote from this species and the few others with racemose inflorescences.

Embelia Burman f.

Embelia acuminata sp. nov. § *Micrembelia.*

Frutex glaber; foliis coriaceis vel subcoriaceis, oblongis ad oblongo-ovatis vel ovato-lanceolatis, 3 ad 7 cm. longis, 1 ad 2.5 cm. latis, tenuiter acute acuminatis, basi acutis, nitidis, in siccitate plerumque pallidis, utrinque distincte punctatis, nervis primariis utrinque 6 ad 8, supra leviter elevatis, haud conspicuis, subtus obsoletis vel subobsoletis; petiolo 5 ad 8 mm. longo; inflorescentiis axillaribus, brevibus, usque ad 10-floris, junioribus fasciculatis, vetustioribus racemosis, rhachibus crassis, usque ad 3 mm. longis et 1.5 mm. diametro, cicatricibus distinctis instructis, squamulis paucis, late ovatis, circiter 1 mm. longis; pedicellis 2 ad 4 mm. longis; floribus 5-meris, sepalis oblongis, obtusis ad acutis, 1 mm. longis, perspicue glandulosis; petalis lanceolatis, sub-

obtusis, circiter 3 mm. longis, basi brevissime (0.5 mm.) connatis, perspicue glandulosis; filamentis circiter 1 mm. longis cum antheris eglandulosis; ovario glabro, glanduloso; fructibus junioribus subglobosis, circiter 5 mm. diametro, punctato-glandulosis.

Indo-China, Tonkin, Chapa, *A. Petelot 1779, 1936* (type), April, 1925.

A strongly marked species manifestly belonging in the section *Micrembelia*. Among the described species it is perhaps most closely allied to *Embelia Fordii* Mez, of southeastern China, yet has little in common with that species. In habit it is a small shrub, erect or possibly scandent, the main stem on one of the specimens being about 5 mm. in diameter.

Embelia polypodioides Hemsl. et Mez *in* Notizbl. Bot. Gart. Berlin, vol. 3, p. 108, 1901; Hemsl. *in* Hook. Ic., vol. 28, pl. 2725, 1901; Mez. *in* Engl. Pflanzenreich, vol. 9, p. 325, 1902.

Indo-China, Tonkin, Chapa, *A. Petelot 1790*, April, 1925. A very strongly marked species previously known only from Yunnan Province, China.

SYMPLOCACEAE

Symplocos Jacquin

Symplocos olivacea sp. nov. § *Bobua, Lodhra.*

Arbor parva, ramis glabris, ramulis junioribus 1.5 ad 2 mm. diametro, adpresse cinereo- ad subferrugineo-hirsutis; foliis in siccitate olivaceis, nitidis, utrinque subconcoloribus, ellipticis ad oblongo-ellipticis, subcoriaceis, 7 ad 10 cm. longis, 3 ad 4 cm. latis, integerrimis, apice acute acuminatis, basi late acutis, subtus parcissime adpresse hirsutis glabrescentibus, costa supra impressa, nervis primariis utrinque circiter 9, tenuibus, distinctis, arcuato-anastomosantibus, reticulis laxis; petiolo parcissime hirsuto, circiter 3 mm. longo; inflorescentiis axillaribus, quam petiolo vix longioribus, cinereo-pubescentibus, paucifloris, plerumque haud ramosis; floribus sessilibus, bracteis late ovatis, dense pubescentibus, 1 ad 1.3 mm. longis, calycis tubo crasso, circiter 1 mm. longo, lobis 5, late ovatis, pubescentibus, vix 1 mm. longis; petalis 5, oblongis, 3.5 mm. longis, extus parcissime pubescentibus; filamentis circiter 40, liberis vel subliberis, glabris, circiter 4 mm. longis; disco protruso, 1.5 mm. diametro, dense cinereo-pubescenti; ovario 3-loculari.

Indo-China, Tonkin, Mau Son, *A. Petelot 1902*, leg. *Du Pasquier*, October, 1924.

Rather unusual in *Symplocos* because of its leaves being strictly olivaceous when dry, in this character resembling those species of the

section *Cordyobaste* rather than most of those in *Bobua*. The species, however, belongs in *Bobua, Lodhra,* and is further characterized by its very short, simple, rarely branched, few flowered spikes which scarcely exceed the petioles in length and which are densely cinereous-pubescent, as is the prominent, somewhat protruding, almost hemispheric disk. It is clearly different from the various species recently described from Indo-China by Guillaumin, and I cannot refer it to any of those considered by Brand.

GENTIANACEAE

Crawfurdia Wallich

Crawfurdia Pasquieri sp. nov. § *Dipterospermum.*

Herba scandens, glabra, ramulis 4-angulatis; foliis lanceolatis, tenuiter acuminatis, chartaceis ad subcoriaceis, integris, 4 ad 7 cm. longis, 1.5 ad 3 cm. latis, basi acutis, 3-nerviis; floribus axillaribus, longe pedicellatis, plerumque solitariis, 4.5 cm. longis; calycis tubo haud carinato, 12 mm. longo, basi cuneato, lobis 5, lanceolatis, acuminatis, 7 ad 9 mm. longis; corolla 4 ad 4.5 cm. longa, lobis 5, lanceolatis, acuminatis, circiter 4 mm. longis.

Indo-China, Mau Son, *A. Petelot 1904,* leg. *Du Pasquier,* October, 1924.

A species belonging in the group with *Crawfurdia speciosa* Wall. from which it differs notably in its longer calyx lobes. From *Crawfurdia Delavayi Franch.,* it differs in its calyces not being at all angled or keeled, and in its longer calyx lobes. The smaller flowers and non-carinate calyces at once distinguish it from *Crawfurdia Trailliana* Forest and *G. Bulleyana* Forest. The genus is new to Indo-China.

GESNERACEAE

Trichosporum D. Don

Trichosporum macranthum sp. nov. § *Holocalyx.*

Frutex glaber, ut videtur scandens, ramulis teretibus, circiter 3 mm. diametro; foliis crasse coriaceis, oblongis ad oblongo-ellipticis, tenuiter acuminatis, basi acutis, rectis vel leviter falcatis, 8 ad 12 cm. longis, 3 ad 4 cm. latis, nervis obsoletis vel subobsoletis; petiolo 5 ad 8 mm. longo; floribus terminalibus, numerosis, subumbellatis, circiter 6 cm. longis, glabris, pedicellis 10 ad 12 mm. longis, bracteis deciduis; calycibus cylindraceis, 1.6 cm. longis, lobis oblongo-ovatis, subacutis,

3 mm. longis; corolla leviter curvata, superne extus parcissime pilosa vel glabra, lobis ovatis, obtusis; filamentis exsertis, partibus exsertis plus minusve ciliatis, antheris oblongis, 3.5 ad 4.5 mm. longis, ovario glabro, stylo in partibus superioribus (ca. 2 cm.) plus minusve ciliato.

Indo-China, Tonkin, Chapa, *A. Petelot 1638*, July, 1924.

Apparently epiphytic, evidently growing in the mossy forest, the branches below the leaves often with numerous rootlets. Its alliance seems to be with *Aeschyanthus rhododendron* Ridl. of the Malay Peninsula, from which it differs in its larger leaves and shorter calyces.

COMPOSITAE

Ainsliaea de Candolle

Ainsliaea tonkinensis sp. nov. § *Scaposae.*

Herba perennis, scaposa, erecta, 20 ad 40 cm. alta, rhizomate crasso, ad apicem inter petiolis villoso; foliis numerosis, radicalibus, longe petiolatis, plerumque oblanceolatis, glabris vel junioribus leviter villosis, cum petiolis 8 ad 15 cm. longis, 1.3 ad 2 cm. latis, olivaceis, chartaceis, acutis vel obscure acute acuminatis, deorsum angustatis, basi longe decurrentibus, margine distanter (2 ad 6 mm.) calloso-dentatis, dentibus oblongis, crassis, obtusis, patulis, usque ad 1 mm. longis, nervis primariis utrinque 3 vel 4, distinctis; petiolo 2 ad 4 cm. longo; inflorescentiis plerumque solitariis, tenuibus, junioribus leviter villosis, vetustioribus glabris, capitulis paucis, distantibus, plerumque racemose dispositis, vel in partibus inferioribus anguste paniculatis; bracteis foliaceis, lineari-oblongis, 5 ad 20 mm. longis, integris vel majoribus parce calloso-dentatis; capitulis solitariis vel binis, sessilibus vel breviter pedunculatis, circiter 8 mm. longis et 2 mm. diametro, trifloris, bracteis glabris, acuminatis, rigidis, exterioribus circiter 2 mm. interioribus ad 6 mm. longis; acheniis adpresse villosis, circiter 2.8 mm. longis, deorsum angustatis, pappi setis plumosis, 5 mm. longis, subcinnamomeis.

Indo-China, Tonkin, Chapa, *A. Petelot 1767*, April, 1925.

The second representative of the genus recorded from Indo-China, radically different from *A. pteropoda* DC. in its vegetative and indumentum characters as well as in its much smaller heads.

Gynura Cassini

Gynura Colaniae sp. nov.

Herba scandens, glabra vel subglabra, ramis leviter striatis, glabris, partibus junioribus leviter pubescentibus; foliis chartaceis, in siccitate atro-olivaceis, oblongis, glabris, 9 ad 11 cm. longis, 3.5 ad 4.5 cm. latis, basi rotundatis vel in foliis immaturis acutis, haud auriculatis, apice acutis vel leviter acuminatis, margine distanter apiculato-dentatis,

dentibus brevibus, patulis, acuminatis, nervis primariis utrinque 5 vel 6, tenuibus, obscuris, reticulis laxis, obscuris, vel subtus subobsoletis; petiolo circiter 1 cm. longo; inflorescentiis terminalibus, laxis, ramis primariis paucis, ad 15 cm. longis, distantibus, foliis parvis lanceolatis 2.5 ad 4 cm. longis subtensis; capitulis paucis 2 cm. longis, glabris vel subglabris, pedunculis tenuibus, leviter pubescentibus; involucri bracteis extimis paucis, linearibus, 2 ad 3 mm. longis, intimis circiter 10, linearibus vel lineari-lanceolatis, circiter 1.5 cm. longis, 1 ad 2 mm. latis, glabris vel subglabris; acheniis glabris, costatis, circiter 3 mm. longis; pappo candido, setis numerosis, mollibus, 1.5 cm. longis.

Indo-China, Tonkin, Province of Bac Giang, *A. Petelot 1843*, leg. *Mlle. Colani*, March, 1925.

A species manifestly belonging in the group with *Gynura procumbens* (Lour.) Merr. (*G. sarmentosa* DC.), from which it differs in its larger, differently shaped, distinctly toothed leaves, and in its larger heads. Each primary branch of the inflorescence is subtended by a reduced leaf, the whole forming a somewhat leafy, lax inflorescence. There are usually about five laxly arranged heads at the end of each primary branch. The indumentum, when present, is confined to the very young parts the whole plant being nearly glabrous, the pubescence being conspicuous only on the smaller branchlets of the inflorescence.

Elephantopus Linnaeus

Elephantopus spicatus Aubl. Pl. Guin., vol. 2, p. 808, 1775.

Indo-China, Tonkin, Hanoi, *A. Petelot 1369*. A native of tropical America, now very common in the Philippines, occurring also in the Marianne Islands, Formosa, southeastern China, and Java, but not hitherto recorded from Indo-China.

A NEW SPECIES OF PANDANUS FROM FANNING ISLAND

BY

UGOLINO MARTELLI

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A NEW SPECIES OF PANDANUS FROM FANNING ISLAND

BY
UGOLINO MARTELLI

Pandanus Hermsianus sp. nov. § *Keura*

Phalanges druparum magnae, ambitu subglobosae, compressae, supra plano-convexiusculae, 6 cm. spissae, 4.5 cm. crassae, et 9 cm. latae, in tertiam inferiorem partem fibrosae, rotundatae, vix attenuatae, ima basi latae; drupis vel loculis numerosissimis (circiter 17), transverse triseriatis, subprofunde et latiuscule separatis, rotundato-pyramidatis, pentagonis, a sulculo longitudinali percursis, loculis exterioribus satis majoribus, lateraliter acute prominentibus, pentagonis, faciebus latis, subplanis et secus suturas druparum sulco longitudinali profundo excavatis; stigma hippocrepiforme planum ad verticem loculorum situm, in loculis exterioribus latissimum (5 mm.), crassum; endocarpium osseum, plus quam tertiam inferiorem partem et totam latitudinem phlangis occupans, fere 3.5 cm. spissum, superne rimosum, ambitu convexiusculum, inferne truncatum, rimulosum; mesocarpium superum fere 2 cm. spissum, fibroso-medullosum, cavernis extensioribus amplis, ovatis, inferum brevissimum fibrosum.

Fanning Island, eastern Polynesia, a single phalange picked up on the beach by Professor W. B. Herms, August, 1924, communicated by E. D. Merrill, herb. Martelli and herb. University of California No. 276345.

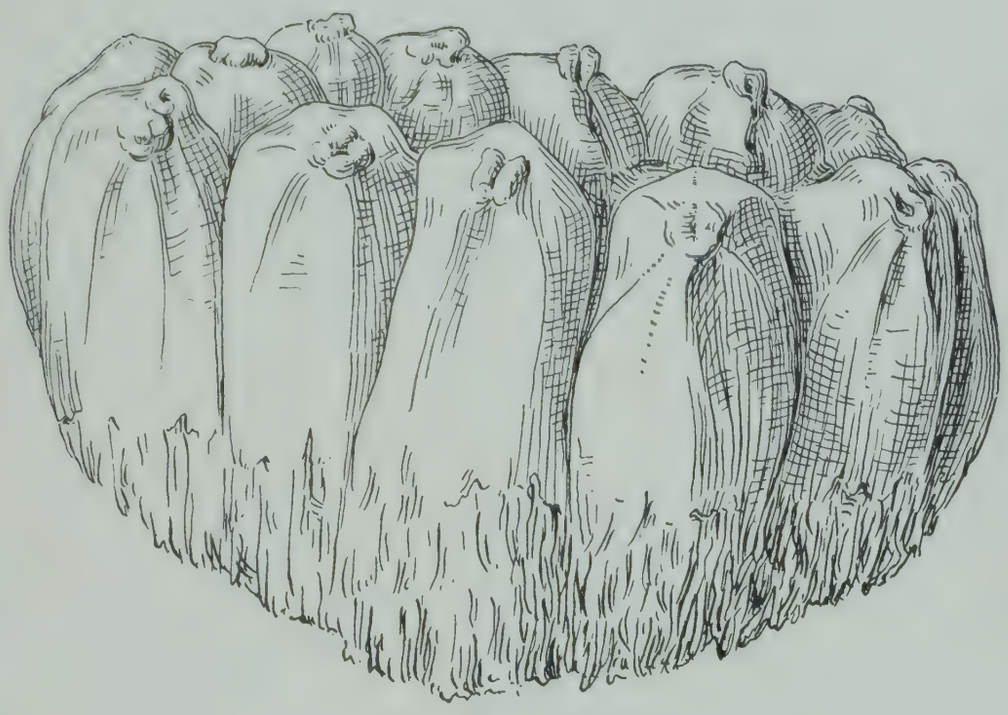
This is a very characteristic species of the section *Keura,* although it is imperfectly known. It is probable that the syncarp is solitary and pendulous, of rather large size, perhaps 20 cm. in diameter, and probably composed of a very limited number of large phalanges. This species and *Pandanus spiralis* R. Br. (non alior.), type from Cape Cliff, Anson Bay, Arnhemland, North Australia, are those in the section *Keura* which have the largest phalanges. In general shape the phalanges of *Pandanus Hermsianus* resemble those of the Australian *P. spiralis* R. Br., save that the locules are not scattered, flat, and contiguous, but mammillate and disposed in three transverse rows, separated from each other by a deep furrow, while the drupes in each row are also separated by furrows.

It is highly probable that this characteristic *Pandanus* is not a native of Fanning Island, or of any of the neighboring small islands, and that the single drupe picked up on the beach originated on some larger island, and reached Fanning Island through the medium of ocean currents.

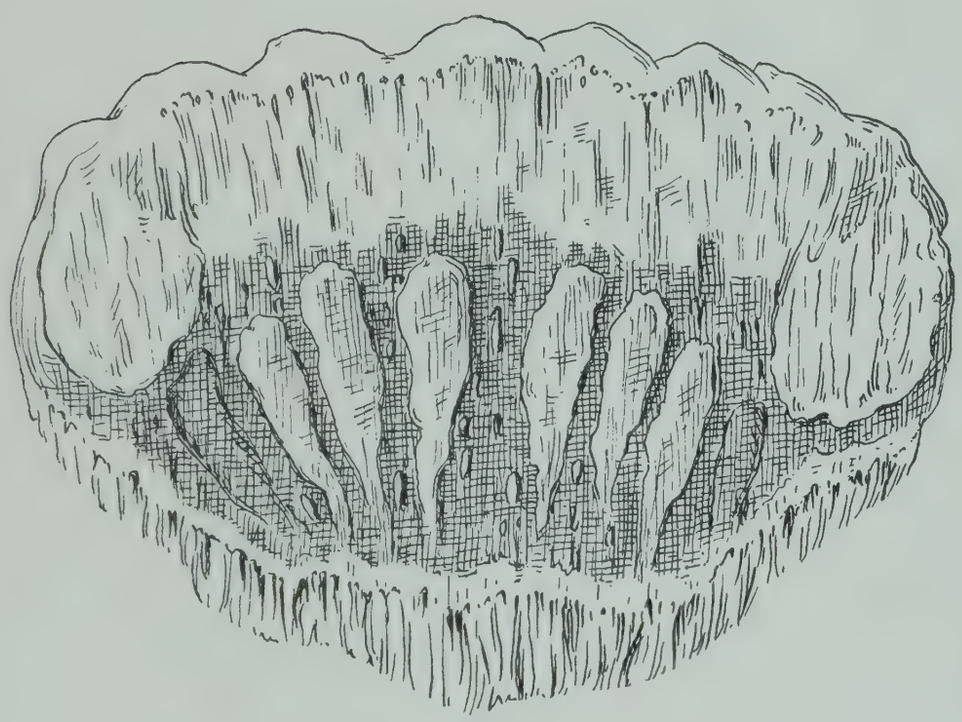
PLATE 12

Pandanus Hermsianus Martelli

A, a single phalange, natural size.
B, transverse section of the same phalange.



A



B

NOTES ON MICRODICTYON. II

BY

WILLIAM ALBERT SETCHELL

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NOTES ON MICRODICTYON. II

BY
WILLIAM ALBERT SETCHELL

My "Notes on Microdictyon" (Univ. Calif. Pub. Bot., vol. 13, pp. 101–107, issued Sept. 28, 1925) were preliminary in nature and intent and were written when it seemed improbable that further information, concerning type specimens in particular, could be obtained other than by a personal trip to Europe. Very soon after publication, however, type specimens of several species were obtained on loan, as well as photographs, notes, etc., of or concerning others, until I am in a position reasonably favorable to complete a survey of the existing situation of the species of the genus. Dr. G. Hamel, of the Laboratoire de Cryptogamie of the Museum nationale d'histoire naturelle of Paris, Professor R. Viguier of the Institut Botanique of the University of Caen, Professor Harald Kylin of the University of Lund, Dr. F. Boergesen of the University of Copenhagen, Mr. A. Gepp of the British Museum of Natural History at South Kensington, Dr. Yamada of the University of Tokyo, and Dr. K. Okamura of the Imperial Fisheries Institute of Japan have, each and every one, contributed or loaned specimens, photographs, drawings, or notes on types or specimens noted in the literature. Dr. Anna Weber-van Bosse of Eerbeek, Holland, has kindly loaned her large collection of specimens of *Microdictyon,* including all those of the Siboga Expedition, reported on by the late Major Theodore Reinbold. The collections of the Farlow Herbarium, examined through the courtesy of Professor Roland Thaxter, had already been examined and were partially reported on in my first paper. To all of these colleagues and the institutions they represent, I return my grateful acknowledgments.

Photographs and drawings of all the specimens have been made or prepared and my studies have reached a point where further report is possible. An extended journey, however, will prevent the complete and finished account being issued at this time, and this will also be delayed in the hope that I may enjoy the opportunity of studying several species in their native habitats and type localities during my trip. It seems best, therefore, to summarize the situation in *Microdictyon* as revealed by the herbarium studies of the very considerable material made accessible since September, 1925.

In my first arrangement I recognized 15 species, two of which were ranked as "species of uncertain position." One of the two species thus ranked as "uncertain" is the type of the genus. *Microdictyon Agardhianum* Dec'ne. It is gratifying to report that what appears most certainly to be Decaisne's type has been found at the University of Caen and the privilege of examining it accorded to me. The second species of "uncertain position," *M. Kraussii* J. E. Gray, has been studied in a topotype agreeing with sketches and notes on the type specimen itself. I have been able to examine either the actual type or a topotype agreeing with descriptions, photographs, drawings, notes, etc., of each of the 13 other species included in my first report. I am proposing 3 new species in the present report, making 18 species in all recognized among the Microdictyons I have studied. The following arrangement of these 18 species is proposed and there are given distinctive characters such as may be most readily expressed in the form of a key.

A Revised Analytical Key to the Sections and Species of Microdictyon

1. **Eumicrodictyon.** Attachments by annulate membranes at the tips of unmodified segments; branching opposite or alternate, rarely stellate.
   1. Primary filaments prominent ..... 1. **M. Agardhianum**
   1. Primary filaments not at all or only slightly and irregularly prominent 2
      2. Filaments decidedly torulose ..... 2. **M. Boergesenii**
      2. Filaments slightly if at all torulose 3
   3. Network lax, meshes commonly 0.5–1 mm. in diameter ..... 3. **M. laxereticulatum**
   3. Network medium, meshes commonly 0.3–0.4 mm. in diameter.... 4. **M. tenuius**
2. **Calodictyon.** Similar to *Eumicrodictyon*, but stellate branching at regular and frequent intervals.
   * **Atrovirescentes.** Fronds rigid, dark blackish-green.
   1. Primary filaments neither regularly prominent nor uniformly so; membranes of the segments hyaline or only tinged with yellow 2
   1. Primary filaments uniformly prominent; membranes of the segments distinctly yellow 4
      2. Fronds ample (even up to 30 cm. broad), commonly deeply split ..... 5. **M. umbilicatum**
      2. Fronds small or medium in size, commonly undivided 3
   3. Primary filaments up to 120μ thick ..... 6. **M. calodictyon**
   3. Primary filaments up to 200μ thick ..... 7. **M. obscurum**
      4. Primary filaments up to 120μ thick ..... 8. **M. Kraussii**
      4. Primary filaments up to 200μ thick ..... 9. **M. nigrescens**
   ** **Laetevirescentes.** Fronds delicate, light yellow-green.
   1. Primary filaments up to 120μ in diameter ..... 10. **M. japonicum**
   1. Primary filaments up to 200μ in diameter 2
      2. Primary segments short ..... 11. **M. Thiebautii**
      2. Primary segments long ..... 12. **M. Palmeri**

3. **Cystodictyoides.** Branching secund ..... 13. **M. Vanbosseae**
4. **Macrodictyon** (J. E. Gray *p. p. max.*): Attachment by fibulae (crenellated membranes) on the tips of unmodified segments.
   1. Membrane of segments thin 2
   1. Membrane of segments thick 3
      2. Primary filaments 250–300μ thick ..... 14. **M. pseudohapteron**
      2. Primary filaments 400–500μ thick ..... 15. **M. Okamurai**
      3. Primary filaments commonly up to 500μ thick, ultimate segments 180μ thick ..... 16. **M. Velleianum**
      3. Primary filaments commonly up to 800μ thick, ultimate segments 300μ thick ..... 17. **M. crassa**
4. **Boodleoides:** attachment by modified segments with crenellated disks (tenacula) ..... 18. **M. Montagnei**

The cruciately branched group, *Eumicrodictyon,* seldom shows any trace of stellate branching.

The distribution of the species of this group (1 to 4) is from the Red Sea, across the Mediterranean to the West Indies. *M. Agardhianum* Dec'ne is known only from the Red Sea, *M. Boergesenii* Setchell from the Canaries and West Indies and possibly south Mediterranean, *M. laxereticulatum* Setchell, north Mediterranean, while *M. tenuius* (Ag.) Dec'ne is known only from Cadiz. The species are closely related and may finally be reducible in number. Boergesen (Mar. Alg. Canary Is., I, pp. 116–120, 1925) has already commented on this aspect of the case and I agree with him that the specimens upon which he based his argument are very close, viz., what I call *M. tenuius* and *M. Boergesenii.* Both, however, seem to me clearly distinct from *M. Agardhianum* of the Red Sea and from *M. laxereticulatum* of the northern Mediterranean. *M. Agardhianum* has a more pronounced venation and much shorter segments (proportionally) than any one of the other three species of the group.

The distribution of the *Calodictyon* group including annulate species with frequent and regular stellate branching, extends from the Atlantic (Canary Islands) to South Africa (Natal) and through the East Indies to the north and south Pacific Ocean. It seems to be divisible, according to color and texture, into two series, the one rigid, very dark green, almost black, and the other of delicate texture, thin, and light yellow-green. The dark green species include *M. calodictyon* (Mont.) Dec'ne (Canary Islands), *M. Kraussii* J. E. Gray (Natal), *M. nigrescens* (Yamada) Setchell (Formosa), *M. obscurum* J. Ag. (Loyalty Islands), and *M. umbilicatum* (New South Wales). In the *Atrovirescens* series, we find 5 species, closely related, but differing sufficiently to be considered distinct, at least for the present.

The light green series (*Laetevirescentes*) includes 3 species, confined to the Pacific and northeastern Indian oceans. *M. japonicum* Setchell, with the most slender filaments of the three, occurs in Japan, on the Borneo Bank in East Indian waters, and possibly also at Easter Island (cf. Boergesen, Algae of Easter Island, p. 253, fig. 5, sub. *M. umbilicatum*), *M. Thiebautii* Setchell, with shorter primary segments, at the Loyalty Islands, and *M. Palmeri* Setchell, with longer primary segments, on the shores of Guadelupe Island in the eastern Pacific.

Microdictyon Vanbosseae Setchell is so distinct in habit and appearance from all other species of the genus as to raise doubts as to whether it may not be referred to a genus of its own. Only two collections are available, both in the herbarium of Dr. Anna Weber-van Bosse. Both were studied by Major Reinbold and noted in the Algae of the Siboga Expedition as "*Microdictyon* sp. nov." The habit of the specimens of the two collections is so different that Reinbold was uncertain as to whether he had one or two species before him. Both, however, have the same type of secund branching, forming wedge-shaped reticulate pinnules, showing two kinds of meshes, the more numerous small and triangular or polygonal, the occasional large and nearly circular. The large circular meshes distributed here and there, but with some regularity, give the frond the appearance of a species of *Cystodictyon*, but the "holes" are situated in an open network instead of an otherwise closed membrane. I have, therefore, segregated this species in a section of the genus which I have named *Cystodictyoides*. Both collections are from the East Indies, that from Lirung showing the cuneate pinnules arranged in an interrupted fashion along a main filament, while the specimens from Borneo Bank show them combined into a strap-shaped frond.

The group of species showing fibulate attachments includes 5 or perhaps 6 species of the Indian, Pacific, and western Atlantic oceans. They resemble the annulate species in not having the attaching segment modified in either shape or size, thus resembling *Cladophoropsis*. They resemble the tenaculate group, *Boodleoides*, in having the attaching membrane crenate or deeply crenulate or laciniate, but differ in not having a specialized attaching segment. For the most part, their segments are coarser and more robust than those of the other species of *Microdictyon*, at least in appearance. The better known species become prostrate and rooting, producing from the prostrate portion erect laminae which are rosulate and rigid, a habit

unknown among species of other sections of the genus. Herbarium specimens generally give little evidence of this peculiar habit, so that its uniformity among the species of the section is not established. The differential characters seem largely those of measurement which, taken alone, allows a certain amount of seeming intergradation, which study of more ample and living material may tend to intensify or possibly to eliminate. The coarsest species are those of the western Atlantic and northern central Pacific and the more delicate species those of the Indian Ocean. As I interpret the confused expressions of J. E. Gray (Seemann's Jour. Bot., vol. 4, p. 292, 1866), his genus *Macrodictyon* was founded largely upon the Sandwich Island plant (*M. Velleianum*), although he included *Cystodictyon Leclancherii* (Martens) J. Ag. within the same genus.

Microdictyon Montagnei Harvey must be separated from the rest of the species referred to *Microdictyon* because of its possession of modified short attaching segments or tenacula. Because of this and some other resemblances to species of *Boodlea,* I have placed it in a separate section of *Microdictyon* which I have named *Boodleoides.*

The normal or at least most striking frond of *M. Montagnei* is flat, or nearly so, but there is a tendency towards a departure from this since the "opposite" branchlets, at least, are similar to those of *Boodlea composita* in being approximate in insertion on one side of the filament although divaricate as they grow outward. The outer pinnules often elongate, have alternate, non, or slightly coalescing branchlets, anastomosing irregularly, and approach *Boodlea paradoxa* Reinbold in their characteristics. The various specimens of the Siboga Expedition referred by Reinbold to this species vary from typical *Microdictyon Montagnei* to seemingly typical *Boodlea paradoxa.* The distribution of *Microdictyon Montagnei* is central south Pacific and East Indian.

It remains to conclude this second series of notes, still preliminary to a final report, with descriptions of the new species indicated in the outline.

Microdictyon laxereticulatum sp. nov.

Laetevirescens; thallo irregulari (fragmentis solummodo visis), usque ad 6 cm. latis et 3 cm. longis, partibus basalibus deuntibus, reticulis venas primarias conspicuas non ostendentibus, areolis magnis trapezoideis, 1–2 mm. diam., magnitudine formaque prope uniformibus; ramifactione oppositis aut singula patentique, numquam (?) stellata; filamentis primariis usque ad 160μ diam., segmentis usque ad 2- (raro 3)-plo longioribus, membranis tenuibus (2μ crassis), hyalinis; filamentis secundariis usque ad 140μ crassis, segmentis usque ad 3-plo longioribus; ramulis ultimis liberisque basi 80μ crasssis ad apicem obtusam lente attenuatis, vulgo 4-plo longioribus; ramis ramulisque anastomosantibus frequenter lente curvatis.

Bajae, near Naples, 1878 (Type Herb. Univ. Calif., No. 74780); apparently of the same collection in Herb. Weber-van Bosse, labeled "Bajae, 9, 1878, legit Fr. Schmitz."

Microdictyon laxereticulatum is of such decidedly coarser mesh than any other of the *Eumicrodictyon* group that it seems desirable to keep it distinct from even *M. tenuius* and *M. Boergesenii,* its nearest relatives. All three of these species, however, may possibly be considered as belonging to one larger species, but are not to be united with *M. Agardhianum,* which may be distinguished by its distinct venation as well as by the much shorter segments of the filaments of each order of branching.

Microdictyon Thiebautii sp. nov.

Laetevirescens; thallo orbiculari usque ad orbiculari-ovato, crispo, imperfecte ad chartam adhaerente, 4.5 cm. lato et 5 cm. alto, marginibus late lobato et laciniato, basi lateraliter umbilicato et ad Melobesieas per filamentos descendentes rhizoideos affixo; ramificatione oppositis, singulis, et stellatis plus minusve regulariter ordinatis; filamentis primariis infero e basi radiantibus et inter se plus minusve liberis, supero flabellatis et inter se per ramos curtiores longioresque connexis, prominentibus et venationem distinctam efficientibus; areolis triangulis aut rhomboideis usque ad polygonis, 100μ usque ad 200μ diam., aut in areolis triangulis parvioribus; segmentis filamentorum primariorum basi usque ad 200μ diam. et 600μ longis, supero 200μ diam, et 160–200μ longis, secundariorum usque ad 120μ diam. et curtioribus quam latis, ultimis liberisque basi 60–100μ diam. et apice 45μ diam., obtusis, 180–240μ longis.

Lifue, Loyalty Islands, M. Thiebault, 1869. Type specimen in Herb. Mus. Paris.

Microdictyon Thiebautii differs from *M. japonicum* and *M. Palmeri* in having the median segments of the primary filaments both broader and shorter.

Microdictyon Vanbosseae sp. nov.

Laetevirescens; thallo in forma magnitudineque variabili in fragmentis adhuc visis aut prope lineari rectangulari aut elongato segmenta nunc simpliciter nunc composite cuneata ut pinnulas ostendente, usque ad 5 cm. longe et 1.5–2 cm. lato, ad chartam stricte adhaerente, reticulis areolas biformes, multas parvas et triangulas et paucas multo majores rotundatas ostendentibus; filamentis primariis percursis, flexuosis, usque ad 200μ diam., segmentis 200–800μ longis, secunde ramosis, angulis acutis; ramis frequenter curvatis, ramellis ultimis rare liberis, 80–100μ diam.

Microdictyon n. sp., Reinbold, in Weber-van Bosse, Siboga Exp., Mon. 59a, p. 67, 1913.

Lirung, Insel Salibabu, reef, Stat. 133 (type); 320. Borneo Bank, 22–28 fathoms; both specimens in Herb. Weber-van Bosse.

The peculiarities of the new species proposed above arise from the secund branching and the tendency of the branches and branchlets to curve in seeking to attach themselves, for there are very few free branches or branchlets in the portions I have examined. These two peculiarities lead to the formation of cuneate pinnules along the zigzag axis either projecting from it or uniting to form a fairly regular linear frond. *Microdictyon Vanbrosseae* stands in a similar relation to the other species of *Microdictyon* that *Cystodictyon* species do to those of *Anadyomene*. It may seem desirable at some later time to establish for it a new genus.

TOWNSHEND STITH BRANDEGEE

AND

MARY KATHARINE (LAYNE) (CURRAN) BRANDEGEE

BY

WILLIAM ALBERT SETCHELL

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MR. AND MRS. TOWNSHEND STITH BRANDEGEE
Photographed at Northampton, Mass, in 1889.

TOWNSHEND STITH BRANDEGEE AND MARY KATHARINE (LAYNE) (CURRAN) BRANDEGEE

BY

WILLIAM ALBERT SETCHELL

In 1906, shortly after central California had received its baptism by earthquake and fire, there came to the University of California two botanists, husband and wife, who devoted all their accumulations of knowledge to the service of the University and entrusted all their books and specimens to its guardianship. They gave untiringly and unstintedly of their services and of their resources to the herbarium of the University from the time of their coming until that of their passing away. Their generosity and their devotion have placed in their debt all those botanists who in future years will come to the University to study the systematic botany of the western United States and of Mexico—a study made possible because of the rich and abundant material given to the University by these unselfish workers. It seems our duty and our pleasure to place on record in the *Publications* of the University of California this brief memorial of their lives and their work, as a testimonial of appreciation of their voluntary services.

TOWNSHEND STITH BRANDEGEE

1843–1925

Townshend Stith Brandegee was born in Berlin, Connecticut, on February 16, 1843, and died in Berkeley, California, on April 7, 1925. His father was Elishama Brandegee (B.A., Yale, 1833; M.D., Yale, 1838), descendant of Connecticut colonial families, who practiced medicine in St. Louis, Mo., and in Berlin, Conn., and who was also much interested in natural history. His mother was Florence (Stith) Brandegee, of a colonial Virginian family. The Brandegee family was a "Yale" family, several near relatives having graduated from Yale College. Townshend served as private in Company G, 1st Connecticut Volunteers, for two years of the Civil War, prepared for college after his discharge, completed the courses in civil engineering at the Scientific School of Yale University, graduated in 1870 with the Ph.B. degree, and won a prize in German during his senior year.

Of his childhood and early life it seems best to quote the following paragraphs of some autobiographical notes left by him.

"I came into this world two days after Saint Valentine's Day in 1843 at Berlin, Conn., and immediately began to 'grow up.' I soon went to school in a typical New England little red schoolhouse where they hired a new teacher every term, who always made the pupils begin at the first lesson. Consequently in geography we never reached Asia or Oceania and in arithmetic were never bothered by fractions. Finally one new teacher on the first day whipped all the pupils (including myself) except two, and that decided my parents to send me to the Berlin Academy, a private school where everything was taught by one teacher, generally only during the winter months. My father was a country doctor who was interested in botany, knew the names of the native plants, and had made a small collection about St. Louis. An uncle also had a small herbarium of native plants. From my father, I must have inherited a taste for natural history. Like most small boys, I made a collection of birds' eggs and with the help of Wilson's Ornithology became acquainted with the birds of Berlin. My father owned a small farm, of which I have ploughed the field with oxen, cut the grass with a scythe, etc. A change in my life came with the Civil War. At the age of 19 I enlisted in First Regiment Conn. Artillery, Co. G., and served two years until discharged as private in the rear rank. Gen. Grant and I took Richmond.

"My first serious work was the identification of the local ferns. Following this came our Civil War, but as a young soldier there was scant time for herborization and my memories of the southern flora are principally of the big rhododendrons of Virginia, the magnolias along the Appomatox, and the abundance of the blackberries that had overgrown the deserted fields.

"The end of the war brought my portion of the army home almost all suffering severely from malaria, recovery being slow.

"About that time it was difficult to find a teacher for the Berlin Academy, so I took the job for six months and prepared myself for Yale. I entered the Sheffield Scientific School, studied civil engineering and graduated in 1870. At Yale I studied botany under Prof. Eaton and at times worked in his herbarium."

After graduating from college Mr. Brandegee practiced his profession of civil engineer for about eighteen years but was constantly botanizing both for his own amusement and also, at intervals, associating it with his surveying work as part of his official duties. This portion of his life is well epitomized by him in his autobiographical notes, and it seems best to allow him to tell the story.

"Soon after graduation I went to Greeley, Colorado, and finding no work there I was persuaded to go to Cañon City and teach a private school (1871). I taught only about three months and then became County Surveyor, City Engineer. I was recommended by my uncle in New York to Mr. J. H. Redfield, who asked me to collect ferns for him. From ferns we branched into all sorts of plants and during my eight years residence in Cañon City I botanized the surrounding region thoroughly. I got together a herbarium of my own and sent duplicates to Mr. Redfield, who identified them, sending the doubtful ones to Dr. Gray. In 1875 on recommendation of Dr. Gray I was appointed assistant topographer and botanical collector to Hayden's Exploring Expedition of S.W. Colorado. The work was in S.W. Colorado and adjacent to Utah. On the day of our most western travel I collected four new species and was much disappointed when we turned back. The night preceding the Indians made an attempt to steal our mules, but the stilling of the bell attracted our attention before their dull knives had overcome hobbles and buckles, whence 'Recapture Creek.'

"In locating railroad lines and making preliminary surveys I came upon many rare plants. I remember, while staking the railway line on the slope of Mt. Antere a thunder shower forced us to quit, and while seeking shelter in a grove of trees I came upon a colony of *Cystopteris montana,* the only one known in the United States.

"A few years later I joined a railway surveying party and was on the first preliminary survey through the Grand Cañon of the Arkansas (Royal Gorge). Then attached to the Santa Fé Ry. as a member of the engineer corps, I was stationed at La Junta and the upper Arkansas and Santa Fé, New Mexico. Continually, depending on work and the season, I collected plants, sending to Dr. Gray and

Mr. Redfield for names. My knowledge of Colorado flora enabled me to recognize desirable specimens at once. From the Santa Fé Ry., I transferred myself to the Denver and South Park Ry. and was put in charge of location and construction of a division in the Sawatch Mts. The division extended from 7,000 to 11,000 ft. altitude, which gave me a fine opportunity to collect the Alpine flora, which I improved, especially on Sunday. All the men of the engineer corps are paid by the month and have objections against working on Sunday. While stationed on this division I collected logs of wood of trees for Prof. Sargent, who was making a report for the U. S. Census. Some of the specimens were very heavy (100 pounds) and they were sent by mail under a frank until some of the stage drivers protested to the authorities. Next I was put in charge of a locating party and located a railway line from Gunnison City up Ohio Ck. During this work I collected many new species. Winter's snow put an end to the locating work, the railway passed into other hands, and extension stopped.

"One season while living at Cañon City I collected a large quantity of seeds of *Pseudotsuga Douglasii, Abies concolor, Picea Engelmanni* and *P. pungens* for Robert Douglass of the Waukegan Nurseries.

"After leaving railway work I was engaged in making a forest map of the Adirondack Region of the State of New York. Cleveland was the State's governor at the time and as he was a Democrat the Republican papers were finding fault with him. In one of their criticisms I was mentioned as a well known democratic politician. After finishing the New York work I joined the Northern Transcontinental Survey as botanical collector and surveyor for a forest map. This engagement kept me busy in the Yakima Region and Cascade Mts. east of Mt. Ranier of Washington for two years. Next I went to Portland in the interest of the bondholders of the Portland and Willamette Valley Ry. That year I paid no attention to botany. Then, for Prof. Sargent, I went to Montana, Washington, California, and Nevada collecting logs of wood for the Jesup collection, N. Y. Then in company with my brother I went on a pleasure trip to the City of Mexico and finally reached San Francisco. No botany on this junket. I was getting ready for a botanical collecting trip into Mexico when Prof. Sargent asked me to go to Santa Cruz Island and get logs of *Lyonothamnus* and of *Quercus tomentella* for the Jesup Collection, and while getting them I made a complete collection of the plants of the island and also of those of Santa Rosa Island. California became my home state then and botany alone my study and work."

It was in 1888 that Mr. Brandegee went to the Santa Barbara Islands and began the study of the insular floras off the west coast of California (both of Alta, or Upper, and of Baja, or Lower California), to which attention had been called by the publications of Edward Lee Greene.

In 1889, Mr. Brandegee made his first botanical trip into Lower California and began the studies of the flora of Lower California and of adjacent parts of Mexico, extended later to those of southern Mexico, which constitute his principal contributions to botanical literature. It seems best here to quote again from his autobiographical notes.

"In the winter of 1886–7 I came to California at the request of Prof. C. S. Sargent, to superintend the collection of rare or troublesome tree trunks for the Jesup collection of the American Museum in New York—the Museum paying expenses. Collectors had failed to get many of these. They were to be as large as could be obtained, five feet long and in perfect condition. Among the more difficult ones were *Larix Lyallii* from the top of Mt. Stewart, Washington, *Picea Breweriana* from southern Oregon, and *Abies venusta* from the Santa Lucia Mountains—the last one peculiarly difficult. [Mr. Brandegee says that this trunk cost $400 to get out. It was wrapped in rawhide, placed on a sled, two men placed tandem dragged it to the shore, and it was shipped by boat.]

"In 1889 the Academy of Sciences was sending Walter Bryant and Charles Haines on an expedition to Magdalena Bay. At my own expense I accompanied them. From Magdalena Bay we went to Comondu and with a pack train of mules went north to San Quintin and then by boat back to California. I made a large botanical collection during this trip.

"I made many botanical trips to Lower California, one to Magdalena Bay and down the coast by mule to Todos Santos up into the Sierra de Laguna and from Todos Santos to La Paz; one from San José del Cabo and again to the Sierra de la Laguna and to La Paz; several to San José, to the Sierra de San Francisquito, Todos Santos, and Cabo San Lucas. Over the Cape Region I have made many collecting trips. Another collecting trip made during this time was from San Diego to San Quintin and up the high mountain San Pedro Martir. Adding all distances traveled together, I have ridden the whole length of the peninsula on a mule.

"In Mexico proper, I have made trips into Sonora, Sinaloa, Puebla, and Vera Cruz. I have always found the people obliging and kindly, and it is no more fair to judge the Mexican people by their bandits than to rate the Italians by the 'Black Hand' or the French by the 'Apaches' of Paris. On a trip to Sinaloa I stopped with a man named Mateo Morales, who lived near the base of the Cerro Colorado. He guided me to all the good collecting places in his vicinity and took a real interest in me. He liked to talk on religious subjects and had an idea that San Francisco was full of heretics. He asked me if I believed in the devil and I answered him that I had never seen one. He believed in a personal devil sneaking around of nights, but assured me of my safety because he had carved a cross on my bedstead.

"At San José del Cabo, where I have so often been that everybody knows me well, I attended church on Sunday and was accorded especial honors, the padre sending for a chair and seating me on the platform alongside the pulpit, while the congregation was obliged to sit on the floor. It is just possible that the relatively immense sum I dropped in the contribution box may have had something to do with these honors. Religion sits very lightly on the males—they think it good for women and children."

Mr. Brandegee became a member of the California Academy of Sciences of San Francisco soon after coming to California and in that social and scientific circle came to know the scientific men of the Pacific Coast of that day, especially those who made the old Academy building (on Dupont street, now Grant avenue) their home. In particular he was associated with Professor George Davidson, Dr. H. W. Harkness, Dr. Albert Kellogg, Professor Edward Lee Greene, and Dr. Mary Katharine (Layne) Curran. On May 29, 1889, at San Diego, just after his return from his first trip down the peninsula of Lower California, he married Mrs. Mary Katharine (Layne) Curran and with her took a characteristic wedding trip, on foot, to San Francisco, botanizing along the way. This was the first of a number of pedestrian botanizing trips taken by Mr. and Mrs. Brandegee.

Mr. and Mrs. Brandegee made their headquarters at the California Academy of Sciences at San Francisco until 1894, when they established their residence at San Diego, high on the mesa above the town, with a brick building to house their herbarium and a small but well-stocked botanical garden and excellent botanizing territory about it. They gave their botanical library and herbarium to the University of California in 1906, Mr. Brandegee being appointed Honorary Curator, and from that year on they resided in Berkeley. Mr. Brandegee very briefly sums up this period of his life in the paragraphs that follow.

"After many years with the Academy of Sciences my wife and I moved to San Diego. From San Diego I went to San José del Cabo a few times and made a trip on a schooner and botanized the islands San Martin, Guadalupe, San Benito, Cedros, Natividad, San Geronimo, San Roque, and Asunsión. I also made one trip to Mexico to Culiacan, Sinaloa, and made a large collection in the vicinity. While my home was in San Diego, one season I made a forest map of the Teton Forest Reservation of Wyoming. I also have carefully botanized San Diego County, the Cuyamaca Mountains, and Colorado Desert. From San Diego we moved to Berkeley, having given our herbarium and library to the University of California.

"From Berkeley I made one excursion into Mexico, going to the state of Puebla and collecting about San Luis Tultitlanapa. My wife and I have lived in Berkeley about fifteen years and every season have collected in California and Nevada, especially on the Mohave Desert. During my life in California I have made numberless botanical collecting trips, going to all parts of the State."

There are four distinct periods in the botanical activity of Mr. Brandegee which it may be well to mention: during his boyhood and student days; during the practice of his profession of civil engineering, chiefly his work on the flora of Colorado; his work on the flora of the islands of California; and finally his work on the flora of Mexico.

His early botany evidently began under the inspiration of his father and concerned itself with botanizing in central Connecticut. Many of his early specimens are preserved in the Herbarium of the University of California. With zoology and ornithology he included botany and hunted particularly for rare ferns. He is mentioned in the "Berzelius Catalogue" (A catalogue of flowering plants and higher cryptogams growing without cultivation within thirty miles of Yale College. Published by the Berzelius Society, New Haven, 1878), as having made "important additions."

During his employment as an engineer, Mr. Brandegee became well acquainted with the flora of Colorado, collecting flowering plants and ferns and even extending his activities to the mosses and a few of the algae of the mountain streams.

An important feature of the engineering side of Mr. Brandegee's work was his association with the surveys which were directly or indirectly connected with opening up new territory and establishing routes for transcontinental railways or for important links, such as Hayden's Survey of the Territories, the survey of the Royal Gorge, the Santa Fé surveys, and the Northern Transcontinental Survey. He botanized all the while—in Colorado, New Mexico, Arizona, Utah, Wyoming, Montana, Idaho, Washington, and Oregon, paying particular attention to forestry.

As one result of his interest in forestry, he became an expert collector of log specimens for Professor Charles S. Sargent, first in connection with the U. S. Census work and later for the Jesup collection of the American Museum of Natural History. He began this work in Colorado and extended it to Montana, Washington, Nevada, and California. His last activity in this line took him to Santa Cruz

Island off Santa Barbara, California, where he became interested in insular floras and finally determined to retire from engineering work and devote himself entirely to botanical pursuits.

Up to this time he had published little that was original, depending upon others for critical determinations and descriptions of the new species of the plants he collected. When he came to San Francisco and fell under the influence of the group of botanical workers at the California Academy of Sciences, he began to rely more upon himself and from that time on prepared his own reports on the botanical material and data obtained on his various trips. The work on the flora of the Santa Barbara Islands extended itself southward beyond the borders of the United States to the peninsula of Lower California. From just before his marriage to Mary K. Curran, then Curator of the Herbarium of the California Academy of Sciences (1889), and on until their removal to Berkeley (1906), he made many trips into Lower California, and to the islands off the coast, but particularly to the Cape region, and his published results rapidly placed him in the position of an authority on its flora.

In 1894, when the Brandegees changed their residence from San Francisco to San Diego, Mr. Brandegee extended his explorations across the Gulf of California to the states of Sinaloa and Durango. During this interval, Dr. C. A. Purpus started sending plants to Mr. Brandegee from California and adjacent states, but later took up the botany of Lower California, and there began a botanical partnership that was ended only with the death of Mr. Brandegee.

The final period of the Brandegees' botanical activity extended from the time of their removal from San Diego (1906) to Berkeley, where they donated their herbarium and botanical library to the University of California and merged their lives and botanical activities with it. Daily for the rest of their lives, both Mr. and Mrs. Brandegee were to be found at work in the Herbarium of the University and, with the exception of an occasional botanical trip to the mountains or to the desert, this continued to the end of their lives, Mr. Brandegee surviving Mrs. Brandegee approximately six years. It was during these years that Mr. Brandegee issued the "Plantae Mexicanae Purpusianae," of which twelve numbers were completed. These were almost entirely made up of descriptions of new species of plants collected by Dr. C. A. Purpus in the states of Puebla, Vera Cruz, Oaxaca, and Chiapas, of southern Mexico.

Townshend Stith Brandegee

TOWNSHEND STITH BRANDEGEE

Photograpehd about his eightieth birthday, April, 1923.

As a man, Mr. Brandegee was retiring and reticent, holding firmly to his opinions, but never obtruding them upon others. These qualities became more pronounced as he grew older and increasing deafness, together with the loss of the sight of one eye, caused him to withdraw into himself as conversation with others except through written communication became less and less possible. He also suffered from partial paralysis, at times to the extent of being incapacitated, but continued his daily work on his Mexican plants until pneumonia laid him low a few months before his death. His mind remained clear and critical to within a few days of his death.

Mr. Brandegee's botanical work was that of an explorer, chiefly from the floristic side, and his knowledge of the species of the flora of the western portion of the United States and of Mexico was considerable. He had an excellent reading knowledge of Latin, German, French, and Spanish, and a speaking knowledge also of the last. He adhered strictly to the law of the Botanical Congresses that all descriptions of new species should be in the form of Latin diognoses, and labored long and hard to cast them in irreproachable form. In his last years, isolated by his deafness, he was rather a lonely figure, but occasionally became companionable, carrying on what was, of necessity, largely a monologue. He was deeply interested in sports, and until prevented by increasing infirmities attended regularly the baseball and football games between the University of California teams and those of other colleges or athletic clubs.

Mr. and Mrs. Brandegee have left to the University of California a most valuable heritage to perpetuate their memory among its resident and visiting botanists, and this not only in the form of the Brandegee Library and Brandegee Herbarium, rich in type and other authentic material, but in the influence of the example of their generous and unselfish spirit of devotion to the advance of botanical science.

Mr. Brandegee was a life member of the California Academy of Sciences of San Francisco, a fellow of the American Association for the Advancement of Science, a member of the Botanical Society of America, of the Society of Sigma Xi, of the National Geographical Society, and a corresponding member of the Academy of Natural Sciences of Philadelphia and the New York Lyceum of Natural History. He also served as a member of the San Diego Board of Education. He assisted in the foundation of the biological journal, *Zoe,* and

served as editor during the greater part of its existence. Many species were named in his honor, and Cogniaux dedicated to him the genus *Brandegeea,* a member of the Cucurbitaceae.

The life of Mr. Brandegee was modest and unassuming. He sought no official recognition, but the published approval of his colleagues and of fellow-workers in his line gave him unalloyed pleasure. He was quick to acknowledge his own mistakes or slips but not willing to accept meekly what he considered injustice. His mode of life was simple and quiet, although he appreciated unobtrusive attention on the part of his friends and colleagues. His humor was quiet and his enjoyment of that of others was discriminating but sincere.

MARY KATHARINE (LAYNE) (CURRAN) BRANDEGEE

1844–1920

Mrs. Brandegee was a Californian botanist and deeply interested in its flora, of which she had a most detailed knowledge acquired both through extensive journeys over the State and from intensive studies of the literature and type as well as all accessible herbarium specimens. She was thorough in analysis, extremely critical in her attitude, and keen even to sharp as to her comment on the published errors of others. She began her botanical studies under Dr. Hans Hermann Behr, of the College of Pharmacy of the University of California, and worked with Dr. Albert Kellogg, of the California Academy of Sciences, and with Edward Lee Greene, later Professor of Botany in the University of California and later still Professor of Botany in the Catholic University at Washington. She was always an extensive collector and obtained for Dr. H. W. Harkness, long president of the California Academy of Sciences, many of the specimens of California fungi described by him or sent to foreign experts. She assisted Dr. Harkness greatly in making microscopic preparations and studies of the parasitic forms.

She graduated from the Medical Department of the University of California in 1878, but not finding the practice of her profession lucrative and having become interested in the work of the California Academy of Sciences, she became Curator of its herbarium, in which position she continued active until, after her marriage, she and Mr. Brandegee moved from San Francisco to San Diego (1894).

As Curator of the Herbarium of the California Academy of Sciences, Mrs. Brandegee was very active in herbarium work and in exploration. She was also intensely interested in providing a channel for publication of scientific papers. Through her influence, the California Academy instituted a series of Bulletins and she took over the duties and tasks of editorship. To provide even freer discussion and criticism, she also conceived the project of founding the biological journal, *Zoe,* supported at first by Dr. Harkness and Mr. Brandegee, but soon after its inception by Mr. Brandegee alone.

Mrs. Brandegee was an indefatigable collector and established in 1891 a "Botanical Club," which became at once a successful organization and continues even to the present.

Mrs. Brandegee covered much of California in her botanical rambles—Sierras, valleys, Coast Ranges, and deserts. Often alone but later accompanied by Mr. Brandegee, she usually had some definite problem or problems to settle. It is said that the Brandegees made their wedding journey on foot, botanizing along the way. She accompanied Mr. Brandegee on one, at least, of his journeys in the Cape region of Lower California, and even in their later years together they reëxplored the Santa Lucia Mountains, during which trip she had the misfortune to break her leg and had to be carried many miles over very rough country to proper shelter and medical attendance. Mrs. Brandegee paid careful attention to variation and stages of development of the plants of California, particularly in certain groups, such as the Eriogoneae, Œnotheraceae, Boraginaceae, Hydrophyllaceae, Cactaceae, Lupinus, etc., and the Herbarium of the University of California has been enriched with the products of her collecting.

Mrs. Brandegee had many projects in hand at which she worked most industriously, now at one, now at another. She accumulated much material in the way of fragments of types or other critical specimens already published upon and prepared many notes, but she brought little to completion. She was never satisfied with her efforts. She projected a flora of California but her ideas as to species were so broad at times that Mr. Brandegee sometimes humorously remarked that he thought that her flora would finally contain only a single species.

Mrs. Brandegee will best be remembered as a critic, both destructive and constructive. Her mind was keen and her search into detail exhaustive. She had little patience with careless untidiness and her eye caught and held distinctions of importance. She believed in public reproof of errors and attitudes of mind contrary to her own idea of scientific accuracy and method. Well acquainted with the work of Edward Lee Greene on the flowering plants of California, but with entirely antipodal ideas, her reviews of his work were searching and her criticism of his attitude of mind caustic. Hers was at times a bitter pen, but in reality she held little personal antagonism for any length of time. She was fond of animal pets and a great student of their habits. Those who visited the Brandegees at their

brick herbarium and garden at San Diego will remember the beloved pet guinea hen and the friendly sickle-bill thrushes that came at her call. Mrs. Brandegee was a biologist in her sympathies and pursued her specialty of botany only because she found herself obliged to select and limit herself to what she might have time and opportunity of advancing toward tangible results. She sought no official recognition or personal commendation. She labored for the satisfaction it brought to her and for the public good. Her only degree was that of M.D., and she was a member only of the California Academy of Sciences and of the Botanical Club she founded in connection with it. A few species of flowering plants have been named after her, chiefly when she was Mrs. Curran.

As to Mrs. Brandegee's own life, she said little, but has left a short biographical sketch which is transcribed from the records of the California Academy of Sciences:

"I came into the world October 28, 1844, in the wilds of western Tennessee. My father, an impractical genius, afflicted with *Wanderlust*, moved continually till stopped by the western ocean, which we reached before my ninth year. The impossibility of getting farther west, and the necessity of filling the five little mouths he had by that time acquired anchored him at last, and I passed my childhood in the foothills of El Dorado County in much isolation.

"Born Mary Katharine Layne, I married at 22 a Mr. Hugh Curran of Folsom, who died near that place in 1874. Coming to San Francisco the next year, I began the study of medicine, graduating from the Medical Department of the University of California in 1878. A young doctor is not usually overrun with patients, and as a member of the California Academy of Sciences in San Francisco, with considerable spare time on my hands, I began to make myself useful especially about the herbarium, which was in a shocking condition. I began to collect plants in 1882, and the next year was offered the curatorship which I accepted, giving up my small practice and devoting the succeeding ten very active years to the service of the Academy.

"My botanical trips are too numerous to catalogue. By the aid of the railway companies I enjoyed a general pass on the roads, which allowed me to ride on anything from Pullman to engine. Later this was somewhat restricted and confined to the State, but it was of the greatest value in allowing me, without too great expense, to utilize the time of the short desert seasons. My botanizing has been almost confined to the State and adjacent Nevada. The single long trip beyond these limits was in company with Mr. Brandegee and Dr. Gustave Eisen to the Cape region of Baja California in 1893. I returned a month before the other members of the party and was shipwrecked at San Pedro near Los Angeles, the vessel running on the rocks in a foggy night.

"My early activities resulted in the beginning of the Bulletins of the California Academy of Sciences, of which I was the acting editor, but desiring some publication that would allow freer scope to discussion and criticism, "Zoe" was begun for me by Mr. Brandegee and Dr. Harkness. Later Dr. Harkness found it too expensive and Mr. Brandegee took over the control, repaying to Dr. Harkness the sum that he had expended.

"In connection with this journal was founded, I believe, the first Botanical Club on the Coast. It was a very popular Excursion-Club and was continued after my departure for San Diego, by Miss Alice Eastwood.

"My names have been given prominence above that I may explain the many forms. My first name being the same as my mother's, I was never called by it, and on marriage to Mr. Brandegee it was dropped as making an unwieldy combination. Later I find I have a sister-in-law, born Katharine Brandegee, who occasionally writes articles about birds, and being sometimes confounded with her in the east, I have adopted my maiden name.

"With me botany was accidental. I would have preferred the study of birds or more strongly still, the study of insects. Biology in any of its branches has always attracted me greatly, even as a child.

"Everyone should know the names of the organisms common in their vicinity. They are very easily acquired a few at a time. One can scarcely talk or even think intelligently about a nameless object, and their names being learned a certain amount of classification follows almost without effort."

Mrs. Brandegee, then Mrs. Curran, was married to Townshend Stith Brandegee at San Diego on May 29, 1889, and died at Berkeley on April 3, 1920, approximately six years before her husband. She was capable of great friendships and of bitter antagonisms, but her outbreaks of sarcasm were professional rather than personal and she was amazed at those who could not distinguish between the two, to her, very different attitudes. Without compensation and refusing all personal or official recognition or commendation, she labored in the Herbarium of the University of California for fourteen years, as regularly and as faithfully as if she held a salaried position. She gave to it of her best and was content to feel that she had contributed her quota toward a better knowledge of the flora of California.

TOWNSHEND STITH BRANDEGEE
1843–1925

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MARY KATHARINE (LAYNE) (CURRAN) BRANDEGEE

1844–1920

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W. A. S.

ON THE LONGEVITY OF POLLEN

BY

RICHARD M. HOLMAN AND FLORENCE BRUBAKER

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RICHARD M. HOLMAN AND FLORENCE BRUBAKER

A major source of difficulty encountered by those who have studied the germination of pollen and growth of the pollen tube has been the wide variation, in percentage of germination and in growth of tube, in pollens of a given species. Such variation is generally found when the pollen is collected from apparently equally mature flowers on different days or in different, though neighboring, localities, and even when it is taken from flowers of the same age in a given locality and at about the same time.

This great variation, and also the fact that, with most locally available species, the flowering period is so short that pollen of a given species is not obtainable over a continuous period longer than five or six weeks, suggested to us the possibility of using a stock pollen; that is, a pollen of a species known to have a high longevity, thoroughly mixed and stored under conditions most favorable to the retention of vitality, and available locally and in considerable quantity.

The number of species tested by us was about fifty, which is more than 25 per cent of the combined total number of species tested by previous investigators.

In this paper we are publishing (*a*) our data as to maximum longevity of air-dry pollen stored at 17–21° C. and of pollens under a number of constant humidity conditions; (*b*) a list, by families, of all the species (about 220 including our own) for which we have been able to find pollen longevity data, this list giving the maximum longevity of the pollens of these species when stored air dry and under the most favorable humidity conditions, and (*c*) certain tentative conclusions based on our experiments and the data collected from other sources.

For a summary of the literature of pollen longevity up to 1922 the reader is referred to the paper by Knowlton (1922). Knowlton's

summary omits, however, any reference to the paper by Rittinghaus (1886) in which observations of the pollen longevity of twenty-nine species including several having a longevity of two months or more, are reported. In his reference to Molisch's (1893) experiments on pollen longevity, Knowlton gives six weeks as the maximum longevity secured by that observer; whereas Molisch states that six species retained their vitality for periods longer than six weeks, and of these six, one, *Narcissus poeticus*, had a longevity of seventy-two days. Pfundt (1910) gives a somewhat fuller account of the earlier literature than does Knowlton.

Table 1 lists the investigators who have reported pollen longevity of more than two months (sixty days), together with the dates of their papers, the species giving maximum longevity in each case, the conditions of storage, and the period during which longevity was retained. The vitality was tested by the fertilizing power or by germination in culture media without the addition of stigma.

TABLE 1

Author	Year	Greatest longevity observed	Species	Storage conditions
Rittinghaus	1886	76 days	Clivia nobilis	Air dry
Mangin	1886	80 days	Picea excelsa and Narcissus pseudonarcissus	Air dry
Molisch	1893	72 days	Narcissus poeticus	Air dry
Sandsten	1910	6 months	Pyrus malus and Prunus sp.	Air dry
Pfundt	1910	279 days	Pinus sylvestris	Over H_2SO_4
Tokugawa	1914	98 days	Narcissus Tazetta	In desiccator
Roemer	1914	95 days	Streptocarpus, Matthiola, and Antirrhinum	Desiccator, 5–10° C
Adams	1916	3 months	Pyrus malus	Air dry
Horsford	1918	several months	Lilium auratum	Waxed paper and dry place
Knowlton	1922	180 days	Antirrhinum majus*	Air dry 10–22° C
Nohara	1924	105 days	Salix gracilistyla	Desiccator, dark, 10° C
Stout	1924	3 months	Phoenix dactylifera	Air dry

* Knowlton found that this pollen even after 670 days' storage in air was still alive and would germinate in the presence of a fragment of stigmatic tissue. This exceeds by over 400 days any previous records of pollen longevity. Without the addition of stigmatic tissue, however, no germination occurred after 180 days of storage. For obvious reasons, it would be a matter of extreme difficulty to compare pollen longevity of any great number of pollens on the basis of germinating power tested in culture solutions in the presence of stigmatic tissue. The longest retention of vitality as tested in the absence of stigmatic tissue is that reported later in this paper, 336 days plus for *Typha latifolia* stored in a calcium chloride desiccator at 18–21° C.

To the work of Pfundt we owe most of our data as to pollen longevity of different species and our knowledge of the important relations between the humidity under which the pollen is stored and the longevity of the pollen. Although the longevity of 279 days for *Pinus sylvestris* is the greatest reported by Pfundt, he found 50 species, among about 120 tested, with a pollen longevity exceeding sixty days.

MEASUREMENTS OF POLLEN LONGEVITY

The measurements here reported were undertaken, as has been stated, primarily to find a pollen of a species obtainable locally which would maintain its germination powers for several months under storage conditions which could be easily maintained. Table 2 gives the results of longevity tests in which the pollens were stored air dry, i.e., in containers communicating with the air of the laboratory; or under various conditions of constant humidity, as in desiccators containing calcium chloride or varying mixtures of sulphuric acid and water.

The pollens were collected in the great majority of cases and whenever possible from flowers in which the anthers had only recently opened. They were stored in small glass cylinders (so-called shell vials) which were closed with corks. These corks were bored before use and the hole loosely plugged with a thin layer of cotton. The pollens were kept in the dark throughout the storage period and were not subjected to temperatures lower than 17° C. nor higher than 22° C. Germination tests were made in hanging drops of 15 per cent cane sugar solution[1] except in the case of two species, *Ceanothus foliosus* and *Solanum umbelliferum,* for which the previous tests of appropriate germination media had shown a 3 per cent solution to be better adapted. The results of several series of tests are included in the table and accordingly it will be found that not all the pollens were stored under the same conditions. The table makes clear, however, just what the storage conditions were in the case of any pollen. The different conditions are designated as I, II, III, IV, V, and VI. The

[1] Although our choice of this concentration of cane sugar was based on a relatively small number of preliminary tests, the choice is borne out by Pfundt's (1909, table 14) reports on the concentrations favorable to germination in pollen of 148 species. Of that number 142 species germinated in 15 per cent cane sugar, and the six which failed to germinate in that concentration all belonged to families which were not represented among the species which we employed.

conditions of storage corresponding to these designations are as follows:

I. In desiccator over 94.2 per cent H_2SO_4, giving at 18° C. a relative humidity of .005 per cent.

II. In desiccator over 54 per cent H_2SO_4, giving at 18° C. a relative humidity of 27.2 per cent.

III. In desiccator over 37.7 per cent H_2SO_4, giving at 18° C. a relative humidity of 63 per cent.

IV. In dessicator over 15.4 per cent H_2SO_4, giving at 18° C. a relative humidity of 91.6 per cent.

V. Air dry, i.e., exposed to the laboratory atmosphere.

VI. In desiccator over calcium chloride.

It will be noted that the sulphuric acid solutions used are approximately the same in concentration as those used by Pfundt (1922, p. 5) except that for the lowest humidity we employed 94.2 per cent instead of 98 per cent.

The species tested are arranged alphabetically in table 2 which presents the results of the tests that we have made, but in table 3, where some of the data given here are also included, the plants have been arranged according to families.

It is unlikely that the maximum figures given in this table are, except perhaps in a few cases, the actual longevity maxima for the species. In the course of the tests it often occurred that positive results were secured with lots of pollen, samples from which had failed to give any germination on a previous occasion or even in two previous and successive tests. Such irregularities in the behavior of pollen from a given collection probably are chiefly due to a lack of uniformity in the lot of pollen. A thorough mixing of the pollen in a given lot, preferably by some mechanical means, should largely do away with this difficulty. To offset this irregularity of behavior of some pollens, germination tests were made, in most cases for several weeks after the first negative test.

The figures for longevity are therefore not to be interpreted as absolute maxima even for the particular lots of pollen and the given conditions of storage and germination, for there may well have been in any case a few grains which would have germinated after the period recorded as that of maximum longevity.

TABLE 2

Species	Methods of storage	Maximum longevity in days	Method giving maximum longevity	Longevity by method V (air dry) in days
Acer sp.	I–V	18	V	18
Adenostema fasciculatum H. and A.	VI	93	VI	
Arabis virginica L. Trelease	I–V	62	I	16
Aquilegia truncata F. and M.	I–V	76	II	20
Brassica campestris L.	I–V	5	II	
Brodiaea capitata Benth.	I–V	38	I, II	10–
Brodiaea grandiflora Smith	I–V	111	II	55
Castilleja parviflora Bong. var. douglasii Jepson	I–V	91	II	35
Ceanothus foliosus Parry	I–V	35	I, II	27
Clintonia andrewsiana Torr.	I–V	46	I, II	32
Cornus pubescens Nutt. var. californica C. and E.	I–V	30	II	2–
Corylus rostrata Ait. var. californica A. DC.	I–V	40+	I, II	12+
Cyclamen persicum Mill.	V, VI	185	VI	18
Delphinium hesperium Gray	I–V	5	I, III, IV, V	5
Dendromecon rigida Benth.	I–V	13	V	13
Disporum hookeri Torr. Britton	I–V	69	I, II	12
Dodecatheon patulum Greene	I–V	89	I, II	37
Eschscholtzia californica Cham.	I–VI	19	VI	5
Fritillaria lanceolata Pursh. var. floribunda Benth.	I–V	98	I, II	32
Garrya elliptica Dougl.	VI	5	VI	
Hypericum sp.	V, VI	28	V	28
Iochroma tubulosa Benth.	V, VI	10	V	10
Lupinus cystisoides Agardh.	VI	145	VI	
Lupinus latifolius Agardh.	I–V	118	II	52
Nicotiana glauca R. Grah.	V, VI	147	VI	37
Nicotiana sylvestris Spegaz. and Comes.	V, VI	68+	V, VI	68+
Nicotiana sylvestris sealed in ampules with CO_2		205+		
Nicotiana sylvestris sealed in ampules with 3 mm. vacua		205+		
Orthocarpus purpurascens Benth.	I–IV	34	I	19–
Osmaronia cerasiformis (T. and G.) Greene	I–V	110	I	36
Pedicularis densiflora Benth.	I–V	11	I, II, III, V	11
Pentstemon cordifolius Benth.	VI	116	VI	
Phacelia californica Cham.	I–V	42	I, II	16

TABLE 2—(*Continued*)

Species	Methods of storage	Maximum longevity in days	Method giving maximum longevity	Longevity by method V (air dry) in days
Ranunculus californicus Benth.	I–V	2	IV, V	2
Ribes sanguineum Pursh. var. glutinosum Brew. and Wats.	I–V	117	I, II	35
Ricinus communis L.	VI	4	VI	
Rubus parviflorus Nutt.	I–V	74	I, II	30
Sambucus glauca Nutt.	I–V	94	I, II	30
Sanicula bipinnatifida Doubl.	I–V	9	II	9–
Scrophularia californica Cham.	I–V	18	I, III	2–
Smilacina amplexicaulis Nutt.	I–V	76	II	40
Solandra grandiflora Sw.	VI	27	VI	
Solanum umbelliferum Esch.	I–V	41	II	6
Stachys bullata Benth.	I–V	49	II	6–
Thermopsis macrophylla H. and A.	I–V	47	II	17
Trientalis europea L. var. latifolia Torr.	I–V	63	I	49
Trillium sessile L. var. giganteum H. E. A.	I–V	102	II	23+
Tropaeolum majus	V, VI	17	V	17
Typha latifolia L.	VI	336+	VI	
Viola pedunculata T. and G.	I–VI	111	I, II	33
Whipplea modesta Torr.	I–V	93	I, II	11
Zygadenus fremontii Torr.	I–V	95	I, II	33–

This seems all the more likely after examination of the complete records (not published here) of germination tests of some of the longer lived pollens in which the total number of such separate tests is rather large. These show frequently that the percentage of germination remains relatively high for some time and then drops abruptly to zero or more frequently to a low percentage, which may remain very little changed over a period of weeks or months.

The following are a few examples of this sort of behavior:

Pollen of *Viola pedunculata* in a desiccator over 94.2 per cent sulfuric acid on the first, fourth, seventh, and thirteenth days after gathering showed germinations of 52, 39, 42, and 42 per cent, respectively. The percentage of germination dropped to 11 per cent between the thirteenth and eighteenth day, but in the course of the next 93 days the rate of germination remained practically constant. At the end of that period, the pollen being then 111 days old, 10 per cent still germinated.

In the case of *Fritillaria lanceolata*, the pollen, stored under the same conditions as the *Viola* pollen just mentioned, showed after 17

days 17 per cent germination and after 28 days 10 per cent, but in the next four days it dropped to 2.7 per cent. The latter figure was not exceeded in the next 64 days, at the end of which time the pollen, now stored for 96 days, showed 1 per cent germination.

Samples of *Typha latifolia* pollen which had been stored in a calcium chloride desiccator for 71, 94, 116, and 158 days gave respectively 75, 70, 65, and 56 per cent germination. In the course of the next month this dropped to 3 per cent and remained practically unchanged during the next 144 days. At that time observations were discontinued, but this pollen, when 336 days old, showed 2 per cent germination.

Pollens stored air dry showed just as frequently as did the desiccated pollens this sudden decrease in germination percentage with the subsequent long survival of a small percentage of the grains. On account of their generally lesser longevity, these cases were, however, somewhat less striking.

In brief, it may be said, then, that in the case of many pollens each lot consists of a relatively large number of grains which retain their viability for a relatively short period, and a small number, constituting generally less than 10 per cent of the whole, which survive storage several times as long as the others.

The term "maximum longevity" used in the above table means, then, merely that pollen of a species in question may retain its vitality at least as long as the number of days recorded.

The results reported in table 2 show that most of the pollens studied were able to survive several weeks' storage in the air dry condition; that is to say, storage in a place where they were protected from light, from high humidity, and from temperatures varying more than two or three degrees from 18° C. Since the species tested were chosen quite at random, it is probable that the pollens of most of the species in this region (middle western California) will retain their vitality for from one to several weeks when stored air dry in most laboratories.

The greatest longevity in the air dry condition was 68 days for *Nicotiana sylvestris.* The lowest longevities for air dry pollens were less than two days in *Scrophularia californica* and *Cornus pubsecens,* two days in *Ranunculus californicus,* and five days in *Delphinium hesperium* and *Eschscholtzia californica.*

Of the 42 pollens tested as to longevity after air dry storage, the average duration of vitality was about 23 days. Of the 42 pollens

stored both air dry and in desiccators with drying agents the averages were 23 days (air dry) and 62 days (desiccators). Of these 42 species 32 showed, when stored in atmospheres of low humidity, an extension of vitality beyond that of the air dry pollens, and in 10 species the longevity was no greater in the desiccators than when the pollen was air dry. In the 32 cases where low humidity extended longevity the average longevities of the air dry and low humidity pollens were 24 and 76 days, so that it may be said that very low humidity tripled, on the average, the length of life of those pollens which it affected at all. In no case did the longevity of air dry pollen exceed that of the same pollen stored at lower humidities.

In the case of the 37 pollens stored over various concentrations of sulphuric acid the conditions under which the greatest longevity was attained were I in 4 cases, I and II in 14 cases, II in 11 cases, and I and III in 1 case. In the other cases the longevity did not exceed that of the same pollens stored air dry. Clearly the humidity conditions most effective in conserving the vitality of most of the pollens were I and II, with the latter somewhat the more effective.

The greatest longevity obtained through storage at low humidity was 336 days for *Typha latifolia* stored in a calcium chloride desiccator. Next to *Typha* in longevity was *Cyclamen persicum*, stored under the same conditions, with a maximum longevity of 185 days. Among other high values are 147 days for *Nicotiana glauca* and 145 days for *Lupinus cystisoides*.

The greatest relative increase in longevity beyond that of the same pollens stored air dry are 15 times (2 to 30 days) in *Cornus pubsecens*, and 10 times (18 to 185 days) in *Cyclamen persicum*.

The longevity of the *Typha* pollen exceeded by 57 days that of any pollen reported by Pfundt, and by 101 days that of any angiosperm pollen which he tested. It exceeds in fact the greatest longevity which has ever been demonstrated for any pollen with the single exception of that of an *Antirrhinum* pollen which Knowlton (1922) reported as having germinated 670 days after storage. In this case, however, a piece of the stigma of a flower of the same species was placed in the mount. When no stigmatic tissue was present in the germination medium Knowlton failed to get germination with *Antirrhinum* pollen that was more than 180 days old. The pollen of *Typha latifolia* which we used showed a germination percentage of 2 per cent when last tested at the age of 336 days. In view of the fact that its percentage

of germination 144 days earlier had been only 3 per cent and 50 days earlier only 2.5 per cent there is little reason to doubt that its longevity would have proved to be greater than a year had circumstances permitted the continuation of germination tests.

MAINTENANCE OF HIGH GERMINATION PERCENTAGE

For the purpose for which our tests were originally undertaken, the maintenance of a high germination percentage for a considerable period is of greater importance than the great longevity of a few grains in a hundred. Most of the pollens which we used showed relatively early the abrupt falling off in germination rate to which reference has been made. A number, however, had a long initial period (at least when stored at low humidities) of high germination percentage. Thus the pollen of *Rubus parviflora,* which when gathered had a germination rate of 72.4 per cent, showed 60 days later a rate of 59.4 per cent. The pollen in this case had been stored in a desiccator over 94.2 per cent sulphuric acid.

Similarly pollen of *Disporum hookeri* stored at the same humidity as the *Rubus* pollen maintained a relatively high germination rate for almost two months. Pollen of this species which had been stored 1, 12, 20, 40, 48, and 55 days showed respectively germination rates of 31, 45, 45, 21, 48, and 44 per cent.

Of all the pollens tested two species, *Nicotiana glauca* and *Typha latifolia,* would serve best as stock pollens, combining great longevity under easily maintained conditions with high rate of germination maintained over a long period. On account of the time and place of collection of these pollens it was not possible to store them except in the calcium chloride desiccator nor to test their germination percentage until several months after they were collected. The *Nicotiana* pollen gave 82 per cent germination 98 days after collection and 50 per cent when 125 days old. That of *Typha,* tested 71, 94, 116, and 158 days after collection, gave germinations respectively of 75, 70, 65, and 56 per cent.

DISCUSSION OF COMPILED DATA

Up to the time of Pfundt's (1910) experiments upon the influence of humidity on the retention of vitality by pollens, no author had secured data on a sufficient number of species to justify even an

attempt to trace any parallel between longevity and systematic relationship, habitat, or such factors as season of flowering and method of pollination. Pfundt did make some such attempts but with few exceptions the conclusions drawn from his data are not very convincing. The relatively small number of species tested in any given family or ecological group, and the great variability in behavior which most observers have reported as often occurring in pollen of a given species, justify our questioning whether Pfundt's few definite conclusions are well founded. With the idea of bringing together for comparison the pollen longevity data of different observers and thus securing a better basis for judgment, at least as to the relation of pollen longevity and taxonomic alliance, we have collected in table 3 the observations of maximum pollen longevities which we have been able to locate in the literature as well as certain of our own data. This table gives 258 observations relative to 231 species belonging to 175 genera and 23 families. A comparison of the data for the same species secured by different observers makes it possible to check to a certain extent the dependability of the observations in general. The table gives the species grouped in families and in the case of each pollen the name, or an abbreviation of the name, of the observer, together with the longevity of the pollen in the air dry condition. In the case of pollens which were stored at lower humidities the longevity is also given for the most favorable humidity condition under which the pollen was stored.

For the 217 species for which longevities of pollen in the air-dry condition are given in this table the mean longevity is about 26 days. Of the 158 species which have been tested after both air dry storage and storage at low humidities, the mean durations of vitality are 22 days and 70 days. If from these 158 species those pollens are excluded which have no greater longevity in lower humidities than when air dry, the average longevities are 24 days (air dry) and 80 days (in desiccators). Thus, as in the case of the much smaller number of species in table 2, we find here that storage at low humidities triples on the average the longevity of those pollens which it affects at all.

TABLE 3

Family	Species	Reported by	Longevity in days	
			Air dry	At most favorable humidity
Pinaceae	Picea excelsa	Mangin	80	
	*Pinus laricio	Molisch	60	
	Pinus montana	Pfundt	65	272
	Pinus pinaster	Pfundt	68	275
	Pinus sylvestris	Molisch	60	
	Pinus sylvestris	Pfundt	74	279
Typhaceae	Typha angustifolia	Rittinghaus	24	
	Typha latifolia	Pfundt	39	144
	Typha latifolia	Brubaker and Holman		336+
Pandanaceae	Pandanus furcatus	Pfundt	40	92
Sparganiaceae	Sparganium erectum	Pfundt	21	63
Scheuchzeriaceae	Triglochin maritima	Pfundt	3	21
Alismataceae	Alisma plantago	Pfundt	1	1
Hydrocharitaceae	Hydrocharis nymphaeoides	Pfundt	13	13 (air dry)
Gramineae	Alopecurus pratensis	Pfundt	2	2
	Dactylis glomerata	Pfundt	2	3
	Hordeum sp	Anthony and Harlan		48 hours
	Lolium perenne	Pfundt	1	1
	Poa Chaixii	Pfundt	1	1
	Poa compressa	Pfundt	1	1
	Secale cereale	Pfundt	½	½
	Zea mays	Andronescu	Less than 4 hours 24°–30°	32 hours (sat.at.)
	Zea mays	Pfundt	1	1
	Zea mays	Knowlton		3 (11° C.)
Cyperaceae	*Carex paludosa	Pfundt	4	13
	Carex vulpina	Pfundt	3	11
Palmae	Phoenix dactylifera	Stout	77	
Araceae	Arum maculatum	Pfundt	17	46
Cyclanthaceae	Carludovica sp.	Pfundt	7	38
Commelinaceae	Cyanotis sp.	Pfundt	5	9
	Tradescantia virginica	Pfundt	4	40
Juncaceae	Juncus effusus	Pfundt	3	8
	*Luzula angustifolia	Pfundt	5	16
	Luzula campestris	Mangin	3	

TABLE 3—(*Continued*)

Family	Species	Reported by	Longevity in days	
			Air dry	At most favorable humidity
Liliaceae	Aloe longearistata	Pfundt	29	78
	Brodiaea capitata	B. and H.	10−	38
	Brodiaea grandiflora	B. and H.	55	111
	Clintonia andrewsiana	B. and H.	32	46
	Colchicum autumnale	Pfundt	92	229
	Disporum hookeri	B. and H.	12	69
	*Fritillaria imperialis	Molisch	40	
	Fritillaria lanceolata	B. and H.	32	96
	*Hemerocallis flava	Pfundt	11	29
	Hemerocallis fulva	Pfundt	11	26
	Hyacinthus leucophaeus	Rittinghaus	44	
	Lilium auratum	Horsford	42 (waxed paper)	
	Lilium bulbiferum	Molisch	67	
	Lilium bulbiferum	Pfundt	41	142
	Lilium candidum	Molisch	67	
	Lilium candidum	Mangin	14	
	Lilium croceum	Mangin	14	
	Polygonatum vulgare	Mangin	30	
	Scilla (Agraphis) nutans	Mangin	70	
	Smilacina amplexicaulis	B. and H.	40	76
	Tofieldia caliculata	Pfundt	6	30
	Tricyrtis hirta	Tokugawa	12	31
	Trillium sessile	B. and H.	23+	102
	Tulipa gesneriana	Pfundt	37	108
	Zygadenus fremontii	B. and H.	33−	95
Amaryllidaceae	Agave densiflora	Pfundt	32	133
	Clivia nobilis	Rittinghaus	76	
	Galanthus nivalis	Pfundt	42	76
	Haemanthus puniceus	Molisch	30	
	Lycoris aurea	Tokugawa	21	75
	Lycoris radiata	Tokugawa	9	62
	Narcissus poeticus	Molisch	72	
	Narcissus pseudo-narcissus	Mangin	28	
Iridaceae	Iris graminea	Pfundt	20	57
	Iris pseudacorus	Pfundt	12	29
Orchidaceae	Epipactis latifolius	Molisch	23	
	Goodyera repens	Molisch	20	
	Gymnadenia conopsea	Molisch	20	
	Listera ovata	Pfundt	40	164

TABLE 3—(*Continued*)

Family	Species	Reported by	Longevity in days	
			Air dry	At most favorable humidity
Leguminosae	Astragalus cicer	Molisch	12	
	Baptisia austriaca	Rittinghaus	25	
	Colutea arborescens	Molisch	12	
	Coronilla varia	Molisch	15	
	Cytisus laburnum	Molisch	40	
	Cytisus laburnum	Pfundt	40	261
	*Lathyrus latifolius	Rittinghaus	15	
	Lathyrus latifolius	Molisch	13	
	Lathyrus latifolius	Roemer		45+
	Lathyrus odoratus	Crandall	23	
	Lupinus cystisoides	B. and H.		145
	Lupinus latifolius	B. and H.	52	118
	Lupinus perennis	Pfundt	129	260
	Lupinus polyphyllus	Rittinghaus	34	
	Melilotus albus	Pfundt	18	96
	Mimosa Spegazzini	Pfundt	7	42
	Robinia pseudacia	Molisch	30	
	Thermopsis macrophylla	B. and H.	17	47
	Trifolium hybridum	Molisch	12	
	Vicia faba	Pfundt	12	21
Oxalidaceae	Oxalis acetosella	Mangin	1	
Tropaeolaceae	Tropaeolum majus	Pfundt	29	88
Rutaceae	Citrus sp. (Pomelo, tangelo and grapefruit)	Kellerman		4 to 6 weeks
Euphorbiaceae	Mercurialis perennis	Pfundt	29	72
	Ricinus communis	B. and H.		4
Aceraceae	Acer sp.	B. and H.	18	18
Hippocastanaceae	Aesculus hippocastanum	Pfundt	17	72
	Aesculus hippocastanum	Molisch	14	
	Aesculus hippocastanum	Mangin	14	
Balsaminaceae	Impatiens sultana	Pfundt	12	29
Vitaceae	Ampelopsis quinquefolia	Pfundt	13	23
Tiliaceae	Tilia platyphyllos	Pfundt	8	16
Malvaceae	Abutilon Darwinii	Pfundt	14	14 (air dry)
Theaceae	Camellia japonica	Rittinghaus	60	
Guttiferae	Hypericum perforatum	Pfundt	18	81
Violaceae	*Viola odorata	Pfundt	35	235
	Viola pedunculata	B. and H.	33	111
	Viola tricolor	Rittinghaus	26	

TABLE 3—(*Continued*)

Family	Species	Reported by	Longevity in days	
			Air dry	At most favorable humidity
Salicaceae	Salix alba	Pfundt	28	57
	Salix caprea	Pfundt	35	70
	Salix fragilis	Pfundt	18	52
	Salix gracilistyla	Nohara	15 (10° C)	105 (10° C)
	Salix triandra var. nipponica	Nohara	10	73
Garryaceae	Garrya elliptica	B. and H.		5
Betulaceae	Alnus glutinosa	Mangin	21	
	Alnus glutinosa	Pfundt	48	53
	Betula verrucosa	Mangin	37	
	Carpinus betulus	Mangin	7	
	Corylus avellana	Pfundt	40	65
	Corylus rostrata	B. and H.	12	40+
Fagaceae	Fagus sylvatica	Mangin	41	
	Quercus pedunculata	Mangin	24	
Moraceae	Cannabis sativa	Pfundt	2	8
Urticaceae	Urtica dioica	Pfundt	3	4
Loranthaceae	Viscum album	Pfundt	56	89
Aristolochisacea	Aristolochia clematitis	Pfundt	8	10
Polygonaceae	Polygonum bistorta	Pfundt	8	8
	*Rumex acetosella	Mangin	5	
	Rumex acetosella	Pfundt	4	14
	Rumex arifolius	Pfundt	8	21
Chenopodiaceae	Chenopodium bonus Henricus	Pfundt	5	8
Caryophyllaceae	Cerastium vulgatum	Mangin	3	
Nymphaeaceae	Nuphar advena	Pfundt	6	32
	*Nymphaea alba	Mangin	3	
	Nymphaea alba	Pfundt	6	35
Ranunculaceae	*Aquilegia truncata	B. and H.	20	76
	Aquilegia vulgaris	Pfundt	14	92
	*Caltha palustris	Mangin	27	
	Caltha palustris	Pfundt	31	64
	Clematis integrifolia	Pfundt	38	103
	Delphinium hesperium	B. and H.	5	5
	Nigella sativa	Pfundt	4	21
	*Paeonia albiflora	Pfundt	56	157
	Paeonia pubens	Rittinghaus	58	
	Paeonia tenuifolia	Rittinghaus	65	
	Ranunculus acer	Pfundt	7	49
	Ranunculus aquatilis	Pfundt	11	51
	Ranunculus californicus	B. and H.	2	2
	Thalictrum flavum	Pfundt	15	98
	Trollius europaeus	Pfundt	29	124

TABLE 3—(*Continued*)

Family	Species	Reported by	Longevity in days	
			Air dry	At most favorable humidity
Papaveraceae	Dendromecon rigida	B. and H.	13	13
	Eschscholtzia californica	B. and H.	5	19
	Papaver bracteatum	Rittinghaus	16	
	Papaver hybridum	Pfundt	10	49
	Papaver rhoeas	Mangin	20	
	Papaver rhoeas	Pfundt	14	97
Cruciferae	Alliaria officinalis	Pfundt	10	32
	*Arabis albida	Pfundt	22	36
	Arabis virginica	B. and H.	16	62
	Brassica campestris	B. and H.	5	5
	Matthiola sp.	Roemer		95+
Crassulaceae	*Sedum acre	Pfundt	29	143
	Sedum boloniense	Pfundt	31	140
	Sempervivum tectorum	Pfundt	26	194
Saxifragaceae	*Deutzia scabra	Molisch	20	
	Deutzia scabra	Rittinghaus	24	
	Philadelphus floribundus	Rittinghaus	32	
	Ribes sanguineum	B. and H.	35	117
	Saxifraga granulata	Mangin	35	
	Whipplea modesta	B. and H.	11	93
Rosaceae	Adenostema fasciculatum	B. and H.		93
	Fragaria sp.	Crandall	16+ (closed Petri dishes)	
	Gillenia trifoliata	Rittinghaus	48	
	Osmaronia cerasiformis	B. and H.	36	110
	Pyrus communis	Adams	70	
	Pyrus malus	Adams	91	
	Pyrus malus	Crandall	11+ (closed Petri dish)	
	Pyrus malus	Sandsten	183	
	Pyrus malus	Pfundt	38	70
	Potentilla argentea	Pfundt	10	44
	Prunus sp.	Sandsten	183	
	Prunus avium	Pfundt	28	126
	Prunus cerasus acida	Pfundt	40	81
	Prunus padus	Pfundt	15	181
	Prunus spinosa	Pfundt	45	154
	Rubus parviflorus	B. and H.	30	74
	Spiraea filipendula	Pfundt	24	71

TABLE 3—(*Continued*)

Family	Species	Reported by	Longevity in days	
			Air dry	At most favorable humidity
Cactaceae	*Cereus flagelliformis	Pfundt	7	13
	Cereus grandiflorus	Pfundt	8	17
	*Echinopsis Eyriesii	Pfundt	8	8
	Echinopsis Zuccariniana	Pfundt	6	6
Thymeleaceae	Daphne mezereum	Pfundt	45	76
Lythraceae	Lythrum salicaria	Pfundt	13	43
Oenotheraceae	Oenothera biennis	Pfundt	8	8
Hippuridiaceae	Hippuris vulgaris	Pfundt	5	5
Umbelliferae	Sanicula bipinnatifida	B. and H.	9−	9
Cornaceae	Cornus mas	Pfundt	59	74
	Cornus pubescens	B. and H.	2−	30
Ericaceae	*Rhododendron arboreum	Molisch	35	
	Rhododendron (Azalea) indicum	Molisch	47	
	Rhododendron (Azalea) mollis	Pfundt	38	178
	Rhododendron sp.	Rittinghaus	42	
Primulaceae	Cyclamen persicum	B. and H.	18	185
	Dodecatheon patulum	B. and H.	37	89
	Hottonia palustris	Pfundt	13	41
	Primula elatior	Pfundt	56	179
	Primula officinalis	Pfundt	31	158
	Trientalis europea	B. and H.	49	63
Apocynaceae	*Vinca major	Rittinghaus	43	
	Vinca minor	Mangin	55	
Asclepiadaceae	Asclepias cornuti	Rittinghaus	11	
Hydrophyllaceae	Phacelia californica	B. and H.	16−	42
Boraginaceae	Pulmonaria obscura	Pfundt	25	73
Labiatae	Ajuga reptans	Rittinghaus	32	
	*Lamium album	Mangin	6	
	Lamium Galeobdolon	Mangin	6	
	Stachys bullata	B. and H.	6−	49
Solanaceae	Atropa belladonna	Mangin	34	
	Nicotiana glauca	B. and H.	37	147
	Nicotiana sylvestris	B. and H.	68+	68+
	Solandra grandiflora	B. and H.		27+
	Solanum dulcamara	Pfundt	9	41
	Solanum umbelliferum	B. and H.	6	41

TABLE 3—(*Concluded*)

Family	Species	Reported by	Longevity in days	
			Air dry	At most favorable humidity
Scrophulariaceae	Antirrhinum majus	Rittinghaus	36	
	Antirrhinum majus	Mangin	43	
	Antirrhinum majus	Knowlton		180
	Antirrhinum sp.	Roemer		95+
	Castilleja parviflora	B. and H.	35	91
	Digitalis ambigua	Molisch	21	
	Digitalis purpurea	Mangin	37	
	Digitalis purpurea	Rittinghaus.	38	
	Digitalis purpurea	Pfundt	32	172
	Lathraea squamaria	Molisch	30	
	Linaria vulgaris	Molisch	21	
	Mimulus luteus	Pfundt	10	65
	Mimulus sp.	Roemer		65+
	Orthocarpus purpurascens	B. and H.	19	34
	Pedicularis densiflora	B. and H.	11	11
	Pentstemon cordifolius	B. and H.		116
	Scrophularia californica	B. and H.	2	18
	Torenia sp.	Tokugawa	14	67
	Veronica buxbaumii	Pfundt	2	6
	Veronica chamaedrys	Pfundt	11	21
	Veronica speciosa	Pfundt	22	47
	Verbascum phlomoides	Pfundt	14	80
Gesneriaceae	Achimenes sp.	Roemer		65+
	Sinningia sp.	Roemer		65+
	Streptocarpus sp.	Roemer		95+
Plantaginaceae	*Plantago lanceolata	Mangin	11	
	Plantago lanceolata	Pfundt	10	35
	Plantago major	Mangin	12	
	Plantago media	Pfundt	14	68
Caprifoliaceae	Sambucus glauca	B. and H.	30	94
	Viburnum opulus	Pfundt	37	164
Valerianaceae	Valeriana dioica	Pfundt	8	17
Campanulaceae	Campanula medium	Pfundt	40	74
	Campanula persifolia	Molisch	21	
	Campanula trachelium	Molisch	30	
Compositae	Onopordon illyricum	Pfundt	6	8

LONGEVITY AND SYSTEMATIC RELATIONSHIP

From a comparison of the maximum longevities under the most favorable humidity conditions of the various pollens which he tested, Pfundt attempted to draw some conclusions as to the relation between duration of vitality and the taxonomic relationships of the species used.

We have compared the observations on both air dry pollens and those stored at lower humidities and have used as far as possible all the data in table 3. Between these two sets of data there is in general a fairly close agreement. That is to say, those pollens having rather high longevity as compared with other species when stored air dry generally have high relative longevity when under the most favorable humidity conditions.

In the case of eighteen species the table records observations by two or more different observers. These species are *Alnus glutinosa*, *Lilium candidum*, *Narcissus pseudo narcissus*, and *Pyrus malus*, the different observations for which are not in close agreement; *Lilium bulbiferum* with the two reports, 41 days and 67 days; and the following species for which there is close agreement among the authors: *Aesculus hippocastanea*, *Antirrhinum majus*, *Caltha palustris*, *Cytisus laburnum*, *Deutzia scabra*, *Digitalis purpurea*, *Lathyrus latifolius*, *Nymphaea alba*, *Papaver rhoeas*, *Pinus sylvestris*, *Plantago lanceolata*, *Rumex acetosella*, and *Zea mays*. In nine of these last thirteen species the various observations for a single species do not differ by more than four days. Such close agreement, in 13 out of 18 cases, appears to justify our treating these various observers' data as comparable, in spite of the fact that the phrase "air dry" may cover a rather wide range of humidity and temperature. Use of the data on air dry pollens in comparing the pollen longevities of different taxonomic groups seems justified provided that the groups in question are represented by a relatively large number of species and that we do not attach too much importance to a few cases of very low or very high longevity within a group.

UNIFORMITY OF LONGEVITY WITHIN A SINGLE GENUS

Pfundt (1909, p. 21) states that the more closely related the species the greater the agreement in longevity of pollens, and that, within the genera *Pinus, Ranunculus,* and *Sedum,* the pollen longevities under most favorable humidity conditions are approximately the same for the different species tested. However, he had data for only three species of *Pinus* and two each of *Sedum* and *Ranunculus.*

The five observations of air dry pollen of four *Pinus* species shown in table 3 bear out Pfundt's conclusion in regard to *Pinus.* It seems likely, therefore, that most *Pinus pollens* have very high longevity, although the number of species tested is small.

As for *Ranunculus,* it appears that the approximate agreement of the two species which Pfundt tested may perhaps be but a coincidence. We found on two different occasions that *Ranunculus californica* had a longevity of two days or less even under the most favorable moisture conditions.

But in spite of some wide divergences within certain genera and in spite of the small number of species for any of the genera in table 3, there seems certainly to be in most cases considerable agreement between the species of a genus. This seems to be borne out by the data for the genera which are marked by a star in the table. That there may, however, be great differences within a genus is shown by the genera *Brodiaea, Lilium, Corylus, Lupinus, Cornus,* and *Veronica.*

POLLEN LONGEVITY IN DIFFERENT PLANT FAMILIES

In reference to pollen longevities in different orders and families, Pfundt (1909, p. 12) expresses himself as follows:

> Before we can investigate the influence of the alliance to different ecological groups we must consider the question whether any connection exists between the longevity and the resistance of the pollen on the one hand and taxonomic relationship on the other. Such a connection can not be denied in so far as the absolute longevity, that is the longevity under the most favorable conditions, is ordinarily uniformly long or short in the species of a given circle of relationship, short for example in the Helobiae, Gramineae, Polygonales and Opuntiales and long in the Pinaceae, Pandanales, Salicaceae, Fagales, Rosales and Primulaceae.

Since many of the families in table 3 are represented by only a very few genera and species we have considered in this connection only the

ten families listed in table 4. With the exception of the Salicaceae, all these families are represented in table 3 by at least five genera. The Salicaceae are included because data for five species of one of the two genera of this small family are available.

In table 4 is shown the ranking of each of ten families as to the mean longevity of air dry pollen and of pollen at most favorable humidities.

TABLE 4

Rank on basis of mean longevity of air dry pollen			Rank on basis of mean longevity of pollen at most favorable humidity	
Amaryllidaceae	(38 days)	First	Primulaceae	(119 days)
Primulaceae	(34 days)	Second	Leguminosae	(115 days)
Rosaceae	(31 days)	Third	Saxifragaceae	(105 days)
Leguminosae	(28 days)	Fourth	Rosaceae	(101 days)
Saxifragaceae	(27 days)	Fifth	Liliaceae	(86 days)
Ranunculaceae	(25 days)	Sixth	Amaryllidaceae	(75 days)
Liliaceae	(23 days)	Seventh	Salicaceae	(71 days)
Salicaceae	(21 days)	Eighth	Ranunculaceae	(70 days)
Scrophulariaceae	(19 days)	Ninth	Scrophulariaceae	(69 days)
Gramineae	(1 day)	Tenth	Gramineae	(1 day)

In table 4 the ranking of the families according to longevity of air dry pollen and of pollen at lower humidities checks very well except in the case of the Amaryllidaceae. In this family we have to do apparently with pollens of high longevity in the air dry condition whose longevity is not so much extended by lower humidities as it is in many families.

The Gramineae is the only family of the ten which differs very greatly from the others in pollen longevity. The cereals and a number of other grasses have long been recognized as having very short-lived pollen. Apparently belonging in the same class as regards early loss of pollen vitality are the Alismataceae and the Cyperaceae, but the number of species of these families for which we have data is insufficient for even a tentative conclusion. The few species of Commelinaceae and Juncaceae in table 3 also have very short longevities for air dry pollens.

Returning to table 4 we find that the Primulaceae rank very high and that next to them are the three families, Leguminosae, Rosaceae, and Saxifragaceae. Of distinctly lower pollen longevity are the Liliaceae, Ranunculaceae, Salicaceae, and Scrophulariaceae. The high rank of the Primulaceae, Leguminosae, Rosaceae, and Saxifragaceae is in agreement with Pfundt's inclusion of the Primulaceae and Rosales among the groups having long-lived pollens. Except for these groups and the Salicaceae and Gramineae, Pfundt's statements

as to the longevities in different groups seem to be based on an insufficient number of genera and species. No one of the orders, Helobiae, Polygonales, and Opuntiales, which he mentions as having short-lived pollens, nor the Pinaceae and Pandanales, which he includes among those having long-lived pollen, is represented by more than three genera. Mangin's observation of the longevity of air dry pollen of *Picea excelsa* and Molisch's tests of *Pinus laricio* pollen do support Pfundt's conclusion that the pollens of the pine family are mostly long-lived. Our observation of *Typha* pollen longevity also makes more probable the statement by Pfundt that the Typhaceae have pollen of high longevity.

We have refrained from any attempt to interpret the data in table 3 from the biological and ecological points of view. Pfundt (1909, pp. 22–29) has endeavored to do this with his data but without uncovering any definite and clear-cut relationships between pollen longevity and the ecological or biological factors which he took into consideration. It is hardly to be expected that a relation between pollen longevity and such factors as habitat, time of flowering, method of pollination, and the like will be clearly revealed without study of a large number of species chosen with special consideration for the light they may throw upon the particular ecological or biological relation in question.

RETENTION OF GERMINATING AND OF FERTILIZING POWER

A consideration of the duration of vitality in different pollens naturally suggests the question whether pollens which have been stored for a long time and are capable of forming a pollen tube in sugar solutions or other artificial germination media are able to fertilize the ovules of their species if placed upon a receptive stigma. The few statements in the literature relative to this question are not in accord. Sandsten (1910, p. 166) states that not all pollen capable of germination is capable of effecting fertilization, and Knowlton also, (1922, p. 786) states that pollen may be able to germinate and yet be incapable of functioning in fertilization. On the other hand, Nohara (1924, p. 31) says, relative to certain *Salix* pollens, that pollen can be used for fertilization as long as it is able to germinate. Roemer (1914, p. 85) even maintains that in *Streptocarpus* stored pollen which had lost its power of germinating in sugar solutions was nevertheless capable of

fertilizing ovules. This suggests the possibility that pollens of such age that they are incapable of germinating in artificial media may be stimulated by some substance in the stigma to form a tube and, perhaps under favorable conditions, bring about fertilization. The germination of *Antirrhinum* pollen in the presence of stigmatic tissue after 670 days, whereas the same pollen 474 days earlier was incapable of germinating without the presence of stigmatic tissue (Knowlton, 1922, p. 771), also suggests that fertilizing ability may outlast the power to germinate under artificial conditions, even though the pollen 670 days old did not in this case prove capable of bringing about fertilization.

CAUSES OF DIFFERENCE IN LONGEVITY IN DIFFERENT SPECIES

In the pollens of the Gramineae loss of vitality seems to rest, at least in part, on different causes than it does in most other plants. It has been shown that loss of water is one of the principal causes of loss of vitality in grass pollens, whereas in the case of most of the other pollens which have been tested the loss of water which must accompany storage at low humidities extends longevity. But among other than grass pollens there are wide differences in longevity, and we are in almost complete ignorance as to the causes of these differences. This is perhaps not to be wondered at when we consider how little is known of the reasons for loss of vitality of seeds with increasing age, a matter which has been a subject of interest for so much longer a time than has pollen longevity. Knowlton (1922) has studied the relation between the ageing of pollen and moisture loss, respiration, food depletion, and reduction in quantity of certain enzymes. He considers, though not on the basis of any experiments of his own, that the most likely cause of death in pollens is the loss of solubility, after a time, by certain proteins of the protoplasm. Actually the evidence on the question of the causes of loss of vitality in other pollens than those of the Gramineae is insufficient to justify any conclusion. Essential to a solution of this question will be a recognition, such as we have attempted, of certain genera and families with distinctly different pollen longevities. A comparison of the spore walls, water content, physical character, and composition of the contents of the pollens of such contrasting groups of plants may well give a key to the problem.

IMPORTANCE OF EXTENSION OF POLLEN VITALITY

Methods of shipping pollen without loss of its fertilizing power have been in use for some time by the United States Department of Agriculture in the case of citrus (Kellerman, 1915) and other pollens, and also by floriculturists and horticulturists. These have generally involved the retention of vitality by the pollen for a few days or weeks only. The extension of *Cyclamen* pollen longevity by us from 18 to 185 days and of that of the orchid, *Listera ovata,* by Pfundt from 40 to 164 days, suggests the possibility of a much more general practice of pollen preservation and pollen shipment for hybridization purposes. Extension of pollen longevity is important not only because it makes possible the shipment of some pollens over great distances so that crosses may be made between plants separated by many thousands of miles, but it also makes it possible to bridge over the long intervals separating the flowering periods of certain different forms which it is desired to cross. Thus the success of attempts now being made in California to hybridize certain conifers depends very largely upon the possibility of keeping alive the pollen of one species until the pistillate cones of the second form are ready for pollination. Similarly crosses of *Phoenix dactylifera* with other species which, it is believed may give superior date varieties, depends upon the retention of vitality for a considerable time by the pollen of the earlier flowering form.

The increase of longevity of *Typha latifolia* by artificial means to almost a year recalls the practice (Stout, 1924, and Swingle, 1904) by the date-growers of Arabia and of California of keeping male inflorescences of one season in order to pollinate the early female inflorescences of the following season. In spite of the fact that Stout found no evidence of survival of air dry pollens for more than 77 days it still seems not unlikely that the practice had a rational origin. Though the pollen may ordinarily, because of the usual methods of storage, soon lose its vitality, may it not be that under particularly favorable conditions of storage such pollen does sometimes survive and is able, perhaps under the stimulating effect of the stigma (Roemer, 1914, p. 85), to fertilize the flowers of the next season?

SUMMARY

1. With the object of finding a pollen obtainable in large quantities and capable of maintaining a relatively high germination rate over a long period, the authors tested the pollen longevity of fifty angiosperm species stored under various conditions of humidity and at room temperature.

2. In many cases of pollens stored at low humidities the germination percentages fell off rather suddenly after a few days or weeks and then for a long period continued at a relatively constant low rate.

3. When stored air dry most of the pollens survive for from one to several weeks.

4. The mean longevity of the pollens stored air dry was about 23 days. Under the most favorable storage conditions the mean longevity was about three times as long.

5. The maximum longevity observed was 336 days plus for *Typha latifolia* pollen stored over fused calcium chloride. After 158 days from the time of collection this pollen still had a germination percentage of 56 per cent.

6. Table 3 brings together, in so far as the authors have been able to locate them, all the published data on maximum pollen longevity under air dry storage and storage at lower humidities. This table includes 258 observations on 231 species belonging to 175 genera and 23 families.

7. A comparison of the data in table 3 for different genera showed, in agreement with Pfundt, that there is a tendency to uniformity in pollen longevity within many genera although wide variations do occur within some genera.

8. Of nine families, in addition to the Gramineae, for which the amount of data seemed sufficient to justify comparison as to relative pollen longevities, the Primulaceae ranked first. The Leguminosae, Saxifragaceae, and Rosaceae followed the Primulaceae, and the Scrophulariaceae stood last. The Gramineae, as is well known, stand far below any other family for which any but very meager data are available.

9. The relation between germinating power and ability to fertilize, the causes of differences in longevity of different pollens, and the practical application of methods of extending pollen longevity have been briefly discussed.

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NEW RHODOPHYCEAE FROM THE PACIFIC COAST OF NORTH AMERICA. I.

BY

NATHANIEL LYON GARDNER

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NEW RHODOPHYCEAE FROM THE PACIFIC COAST OF NORTH AMERICA. I.

BY

NATHANIEL LYON GARDNER

Helminthora stricta sp. nov.

Fronds very decidedly lubricous, 1–2.5 cm. high, up to 1 mm. diam., irregularly branching; medullary filaments 8–12μ diam., cross-walls moderately frequent; cortical filaments dichotomously to irregularly branched, many remaining unbranched; ultimate branches 7–10 cells long; cells of cortical filaments narrowly fusiform; lower cell of the fertilized carpogonium giving rise usually to involucral filaments as well as do the cells of the carpogenic branch.

Growing on *Phyllospadix,* La Jolla, Calif., June. Type, Gardner, no. 5033.

This species of *Helminthora* is very closely related to *H. Saundersii* of this paper. Both species grow on the same species of host plants and both seem to be very scarce. Possibly the two species may have to be united after study of sufficient material reveals the limits of variability of each.

Helminthora Saundersii sp. nov.

Fronds diminutive, soft and lubricous, 2–3 cm. high. 0.5–1 mm. diam., branching moderately frequent, with branches mostly of the first order, but in part of the second order, all branches approximately of the same diameter; medullary filaments densely crowded, 12–16μ diam., with cross-walls inconspicuous and far apart; cortical filaments 4–5 times dichotomously branched, loosely held together, cells variable in size, mostly fusiform and the terminal ones usually smallest; antheridia in spherical clusters on small branches arising from the terminal cells; carpogonia on three-celled carpogonial branches arising near the base of the cortical filaments and giving rise to involucral branches surrounding the cystocarp; lower cell of the fertilized carpogonium remaining naked; gonimoblasts arising from the upper cell of the fertilized corpogonium, very densely crowded.

Growing on leaves of *Phyllospadix,* Monterey, Calif., July, 1896. Collected by De Alton Saunders. Type in the Farlow Herbarium, Harvard University, Cambridge, Mass.

The type material, consisting of three small groups of mounted specimens, is all that is known of this species. The host is very abundant all along the Californian coast, but apparently no one else has ever noticed the small epiphyte growing upon it. The material is labeled *Helminthora divaricata* in Saunders' writing. It differs from that species in being very much smaller, more lubricous, in having less divaricate, ultimate ramuli, and in having less difference in the length of the branches and the ultimate ramuli than *H. divaricata* as represented by the specimens of *Mesogloia Hudsonii* Wyatt, Algae Danm., no. 99, the plant quoted by J. G. Agardh (1851, p. 416) as being typical of his newly created genus *Helminthora*.

Helminthocladia gracilis sp. nov.

Plate 15

Frond attached by a small disk, about 18 cm. high, with one main central axis and several prominent lateral axes, both main and lateral axes giving rise to numerous shorter branches and these in turn clothed with short (2–5 mm. long) ultimate, divaricate ramuli; central axis about 2 mm. diam. at the base, each succeeding order of branches reduced in size; central filaments densely crowded together, occasionally branched, 9–14μ diam., about 100μ long; cortical filaments 3–5 times dichotomously branched; cells narrowly pyriform; antheridia in dense clusters on the terminal cells of the cortical filaments, 1–2μ diam.; carpogonia on three-celled carpogonial branches near the base of the cortical filaments; gonimoblasts densely congested.

Habitat unknown. Santa Barbara, Calif. Type in the Farlow Herbarium, Harvard University, sub. *Helminthora divaricata*.

The cortical filaments of *Helminthora gracilis* resemble very much those of some forms of *Cumagloia Andersonii* (Farlow) S. and G., but the cystocarp is not widespread among the cortical filaments as in that species. The gonimoblasts are congested into a dense head as in the genus *Helminthocladia*. These, however, are not surrounded by specialized filaments from the carpogonial branch, as in the genus *Helminthora*.

Myriogramma pulchra sp. nov.

Plate 16

Fronds sessile, attached by a small disk, more or less cordate at the base and broadly expanded, deeply lobed and with broad folds; mostly monostromatic but with two to several layers of similar cells at the base, wholly destitute of macroscopic or microscopic veins; color deep rose-pink, irridescent when wet; margins relatively smooth, somewhat sinuous, not denticulate; reproduction unknown.

Growing in the sublittoral belt. Puget Sound, Washington. Type, Gardner, no. 2192 (Herb. Univ. Calif. no. 284029), found cast ashore at Point Defiance, Tacoma, Washington, May, 1910.

The placing of this beautiful red alga in the proper genus is decidedly problematical on account of the absence of any indications of reproductive organs. The absence of a specialized apical cell clearly eliminates it from the Delesseriae and from section "A" of the Nitophylleae as outlined by Kylin (1924). The monostromatic character of most of the frond and the total absence of veins allies it with the genus *Myriogramma* Kylin, where I have placed it for the present, awaiting knowledge of the characters of its reproductive organs.

Since finding the plant in May, 1910, I have revisited the type locality on various occasions at the same time of the year as well as later, but have failed to locate a single plant. At the time of collecting the type material, hundreds of plants were cast ashore, presumably from the sublittoral belt, since search along the shore for two miles when the tide was minus two feet failed to reveal any growing in position. The plants are relatively tough, though very thin and silky, and are beautifully iridescent.

Erythroglossum divaricatum Setchell and Gardner sp. nov.

Plate 17, figure 2

Fronds 1.5–2.5 cm. high, up to 0.5 mm. wide, approximately of the same width throughout except at the very sharply attenuated apices, with smooth margins and divaricate branching, monostromatic at the margins and apical parts, composed of two or more layers of cells in the middle and older parts; midrib and lateral veins absent; surface cells 16–20μ diam.; apical cell narrow and longer than broad; tetrasporangia and procarps unknown.

Pacific Grove, California, probably growing in the sublittoral belt. Type, Mrs. J. M. Weeks, no. 18 (Herb. Univ. Calif. no. 95842), June, 1896.

The type is supplemented by a fragment of a specimen in the Farlow Herbarium collected at Pacific Grove in July, 1896, by De Alton Saunders and labeled *Delesseria*.

Erythroglossum divaricatum is closely related to *E. delicatula* of this paper, differing from that species in being smaller than the type, having smaller cells, divaricate branching with branches more nearly of the same width throughout, and in having sharper apices and longer terminal cells in the cortical filaments.

Erythroglossum delicatula sp. nov.

Plate 18

Fronds from 1–2 cm. (up to 10 cm.) high, 1–2 mm. wide in the older parts, reduced gradually at each order of branches, the terminal or ultimate ramuli 100–200μ diam., and becoming very gradually attenuated to a long, sharp apex, branches of the largest plants from 7–10 orders, irregularly alternate or in part secund; margins smooth; younger parts and margins of the thallus monostromatic, the older parts varying from two to six layers of large cells especially in the oldest stipitate portion; midrib and lateral veins absent; surface cells 22–28μ diam.; apical cell rounded, broader than long; cystocarps relatively large, occupying the width of the frond; tetrasporangia in small sori extending nearly to the margin of the frond.

Growing in the lower littoral and upper sublittoral belts. San Pedro, California. Type, Mrs. H. D. Johnston, no. 139 (Herb. Univ. Calif. no. 94715).

The type material of this species was collected by Mrs. Johnston at San Pedro, California, in June, 1899, "washed ashore." It consists of one large, clean, well developed cystocarpic plant. I collected several specimens of tetrasporic material growing on the government breakwater at San Pedro in the lower littoral belt in January, 1909. These latter specimens are only one to one and a half centimeters high and a fraction of a millimeter wide.

The material conforms to Kylin's idea of the genus *Erythroglossum* as outlined in his monograph of the Delesseriaceae (1924, pp. 30–33) with the exception of the distribution of the tetrasporangia. He states that they are in sori along the margin of the frond, but in this species the sori are in the middle of the frond and do not extend quite to the margins. The fronds, however, are very narrow. Kylin recognizes six species as belonging to this genus, two of which, *E. californicum* J. Ag. and *E. intermedium* (J. Ag.) Kylin, are represented on the Pacific Coast of North America. *E. delicatula* is very much narrower than any of these. Hitherto no cystocarps have been observed in any species of the genus. The cystocarps in this species are relatively large and are typical of the group Nitophylleae as outlined by Kylin. The procarps are numerous in the type specimen and are distributed over the frond, some within two cells of the margin, but the details of their development were not worked out on account of paucity of material.

Membranoptera multiramosa sp. nov.

Plate 19, figure 1

Fronds 3–5 cm. high, 2.5–4 mm. wide, profusely and alternately branched exclusively from the margin; at times much crisped along the margin and the tetrasporic plant bullate; color purplish on drying; midrib moderately conspicuous, decidedly so below, merging into a distinct stipe; side veins numerous, in part composed of several filaments and in part monosiphonous, microscopic, irregularly branched on the lower side, extending for the most part to the margin of the frond and terminating in prominent "teeth"; cystocarps crowned with a fimbriate outgrowth around the ostiole; tetrasporangia in narrow belts along and close to the midrib, extending outward along the veins.

Growing on rocks in sheltered places at the extreme lower littoral belt. Central California. Type, Gardner, no. 4911 (Herb. Univ. Calif. no. 266290), April, collected at Moss Beach, San Mateo County, California.

This species may readily be distinguished by its relatively wide thin fronds, its profuse branching throughout from very close to the base, its finely and profusely denticulate margin and the fimbriate outgrowth from the cystocarp, similar to that found in *Membranoptera dimorpha* of this paper.

Membranoptera Weeksiae Setchell and Gardner sp. nov.

Plate 19, figure 2

Fronds 4–8 cm. high, 0.5–1.5 mm. wide, profusely branched, branches of 4–6 orders, all from the margin, arising at about 45° angle; midrib relatively large and conspicuous, becoming decidedly stipitate at the base, lateral veins indistinct or at times absent; margins smooth, entire; cells of the central part of the midrib about twice as long as broad, relatively large; fruit typical of the genus.

Growing on rocks in the lower littoral and upper sublittoral belts. Central California. Type locality Pacific Grove.

The specimen collected by Mrs. Hall at Santa Barbara and now in the Herb. J. Agardh, no. 31826 (*fide* W. A. Setchell) may belong to this species. *Delesseria alata* C. L. Anderson, Zoe, vol. 2, p. 224, 1891; Howe, Erythea, vol. 1, p. 68, 1893.

I have not had an opportunity to examine any of the material cited in these two publications and therefore cannot speak with certainty as to the correctness of the synonymy. Several collections of this species have accumulated in the Herbarium of the University of

California from various localities along the coast of central California. These have been listed usually as *Delesseria alata*. Superficially they resemble *D. alata* as found growing on the coast of Europe, but the fronds are much narrower. I have carefully compared the structure with that of a specimen of *D. alata* distributed by Wyatt, no. 14, from Torbay, on the southern coast of England, which is probably as nearly typical of the species as can be had, and found the histological characters to be decidedly different. The midrib of the plant from Torbay is much larger, more complex; the central filaments have cells much wider and many times longer, and the cells of the alae are much smaller than those in our plant.

Membranoptera Setchellii sp. nov.

Fronds about 5 cm. high, 2.5–3.5 mm. wide in the older parts, gradually diminishing to the attenuated apices, with well delimited midrib and monostromatic alae wearing away to the distinct midrib which becomes the stipe; lateral veins opposite, indefinite, composed of a single row of cells, at times branched from above and below, many not reaching the margin; reproduction unknown; margins smooth; cells of the alae very unequal in size, angular, and irregularly placed in the main body of the frond.

Collected at Morzyhovey Bay, Alaska. Type, Charles H. Townsend, no. 5776 (Herb. Univ. Calif. no. 93349), 1894.

Pteridium spinulosum Setchell and Gardner, Alg. N. W. Amer., 1903, p. 324 (in part). The plant here quoted as having been collected at St. Paul Island and reported by Ruprecht (1851, pp. 244 and 248) as *Delesseria Beeringiana* var. *spinulosa* is a different plant. Since the publication of the above work by Setchell and Gardner, Setchell has secured a fragment of the plant from St. Paul Island, in the Herb. J. Agardh at Lund, under *Delesseria spinulosa* no. 31820, with an annotation in Ruprecht's handwriting, "*Delesseria Beeringiana* var. *spinulosa*." Examination of this material shows it to be a typical *Membranoptera* but certainly distinct from *M. Setchellii* as here proposed. The margins are decidedly denticulate whereas the margins of *M. Setchellii* are entire and smooth. The cells of the two species are wholly dissimilar. Kylin (1924, p. 16) has referred the Agardh specimen to *Membranoptera denticulata* (Mont.) Kylin.

Membranoptera dimorpha sp. nov.

Plate 17, figure 1; plates 20 and 21

Fronds 8–14 cm. (up to 25 cm.) high, 5–8 mm. wide, with denticulate margins; main branches arising from the margin in the apical portion, relatively few; secondary branches arising from the midrib, relatively abundant, narrowly lanceolate; midrib prominent, lateral veins in part a single series of cells and in part several series of cells, the latter especially so in the tetrasporic plants, opposite, extending to the margin, giving off numerous, more or less irregular, microscopic branched veins of a single series of cells; margins denticulate; antheridial and tetrasporic sori along both sides of the midrib and extending nearly to the margin of the frond along the larger paired veins on both the main branches and on the branches or proliferations from the midrib; cystocarps fairly abundant on both kinds of branches, crowned with a fimbriate prolongation around the ostiole.

Growing on rocks in the extreme lower littoral belt. Queen Charlotte Island to Westport on the west coast of Washington. Type, Gardner, no. 3884 (Herb. Univ. Calif. no. 284025). Neah Bay, Wash., May.

Delesseria quercifolia var. *linearis* Collins *in* Phyc. Bor.-Amer. (Exsicc.) no. 938, 1902, (*Nomen nudum*), collected by Misses Butler and Polley at Minnesota Seaside Station, Port Renfrew, Vancouver Island. This distribution was referred later by Collins (1913, p. 119) to *Pteridium serratum* (P. and R.) De Toni.

Schizoneura quercifolia var. *linearis* Setchell and Gardner, Alg. N. W. Amer., 1903, p. 323.

The *Delesseria serrata* of Postels and Ruprecht (1840, p. 15) from Unalaska, reported by Ruprecht (1851, p. 245) from St. Paul Island and by Saunders (1901, p. 438) from Alaska without recording localities, possibly belongs to this species. I have not had an opportunity to examine any of the material of these collections and as pointed out by Kylin (1924, p. 15) in his excellent work on the Delesseriaceae, the original description is too incomplete for one to render a correct judgment on that alone.

Fortunately the material from Neah Bay is in prime fruiting condition, all three kinds of fruit being represented. The specimens from Queen Charlotte Island are much larger than the other collections but are structurally similar and are in excellent tetrasporic fruit. The margins in all are abundantly denticulate, being in this character similar to *Delesseria serrata* P. and R.

The very distinct character separating this species from others of the genus is the dimorphic character of branching. The principal forking resulting in most of the larger branches takes place near the growing point and from the margin. This character is typical of the genus *Membranoptera*. In addition to these original branches, many narrow branches, some of which are four centimeters long, arise from the midrib as in a typical *Apoglossum* and all branches bear fruit. These secondary branches are not regenerations, such as are sometimes found in old plants, perennial in character, of certain species of the group. In all other respects it seems more like a *Membranoptera* than an *Apoglossum* and I am placing it with the former rather than creating for it a new genus.

Helminthocladia Calvadosii (Lamour.) Setchell and Gardner comb. nov.

Dumontia calvadosii Lamour. *in* Dict. d'Hist. Nat., vol. 5, 1824, p. 643. *Mesogloia purpurea* Harv. *in* Hook. Br. Fl., vol. 2, 1833, p. 386; Wyatt, Alg. Danm. (Exsicc.), no. 47. *Helminthocladia purpurea* (Harv.) J. Ag., Sp. Alg., vol. 2, part 2, 1851, p. 414; Rosenvinge, Mar. Alg. Denmark, 1909, pp. 147–149, fig. 71–73; Hauck and Richter, Phyc. Univ. (Exsicc.), no. 653; Collins, Holden, and Setchell, Phyc. Bor.-Amer. (Exsicc.), no. 686.

The exact type locality of this species apparently has not been recorded. It was known on the coast of France before Harvey published it as *Mesogloia purpurea* in 1833. Chauvin (*loc. cit.*) first called attention to the identity of Lamour's *Dumontia Calvadosii* (*loc. cit.*) and Harvey's *Mesogloia purpurea* (*loc. cit.*) To him it clearly belonged to neither of these genera and in placing it in the genus *Nemalion* he selected Harvey's specific term rather than that of Lamouroux, although the latter clearly has claim to priority and is consequently here restored.

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EXPLANATION OF PLATES

PLATE 15

Helminthocladia gracilis sp. nov. × 1.

PLATE 16

Myriogramma pulchra sp. nov.

CENTIMETERS

PLATE 17

Fig. 1. *Membranoptera dimorpha* sp. nov. × 1.

Fig. 2. *Erythroglossum divaricatum* Setchell and Gardner sp. nov. × 1.

Fig. 1

Fig. 2

PLATE 18

Erythroglossum delicatula sp. nov. × 1.

PLATE 19

Fig. 1. *Membranoptera multiramosa* sp. nov. × 1.

Fig. 2. *Membranoptera Weeksiae* Setchell and Gardner sp. nov. × 1.

Fig. 1

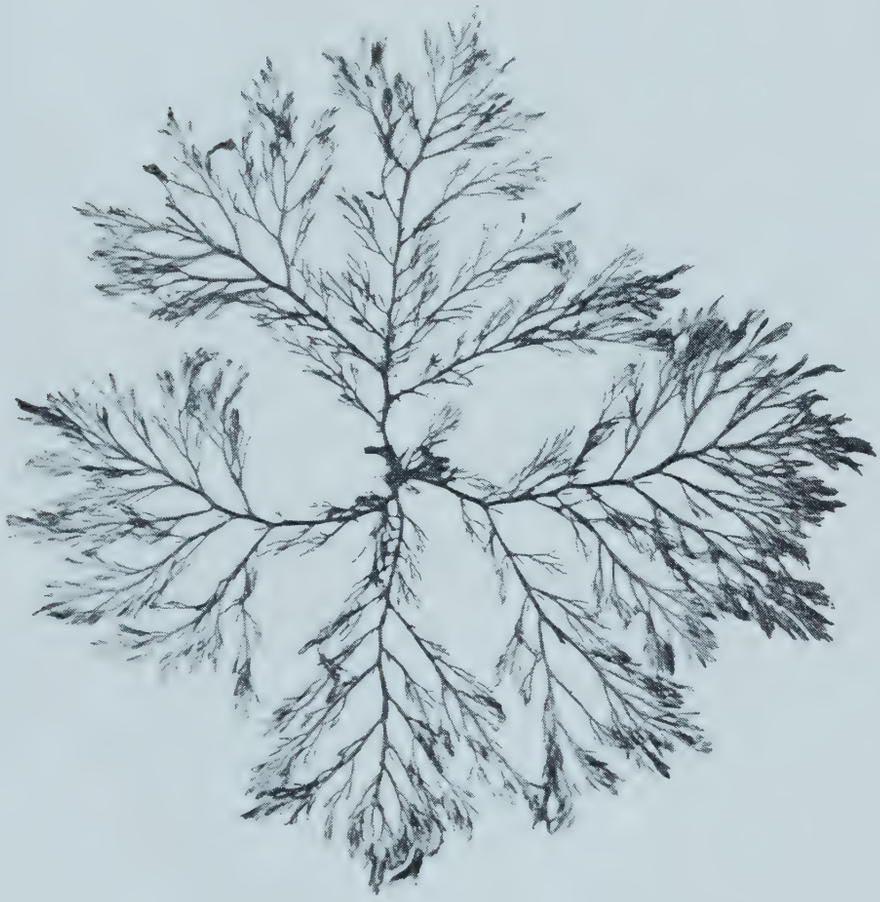

Fig. 2

PLATE 20

Membranoptera dimorpha sp. nov. × 1.

PLATE 21

Membranoptera dimorpha sp. nov. × 1.

THE LOCATION OF THE REDUCTION DIVISIONS IN A CHAROPHYTE

BY

ALBERT HENRY TUTTLE

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THE LOCATION OF THE REDUCTION DIVISIONS IN A CHAROPHYTE

BY

ALBERT HENRY TUTTLE

The members of the Charophyta form a small but important group of plants, than which no other is more distinctly isolated. Its systematic relations to the members of the other and much larger primary groups of plants into which the vegetable kingdom is divided have been at times the subject of much discussion, with conclusions that have varied widely. In the hope of finding some facts that would be of service in the settlement of this vexed question, a study has been made of a decidedly unique member of this interesting group.

The primary purpose of this investigation has been the study from a morphological standpoint of the development, cell by cell when necessary, of the organs of greatest significance and of the regions on which they are borne; and the interpretation of the results thus obtained. Interesting and important as they are, questions of cytology have received special attention only when they bear more or less directly upon the interpretation of the structure and development of the organs under consideration; other cytological details, of equal interest as such, have been left for separate study.

By far the most important of these considered here is the location of the reduction divisions. A brief statement[1] was made in *Science*, October 31, 1924, to the effect that these divisions take place in the apical cell of the oogonium and in the antheridium. This conclusion, at variance with those which had already been announced by others as the results of study (in other species) of the problem, has naturally been received with considerable question. On account of this fact, and of the importance of the subject, it has been deemed expedient to publish separately a brief description, with accompanying illustrations, of some of the observations upon which the statement was based, without awaiting the detailed description of the organs involved which will be made in the larger publication now in preparation.

[1] The use, in this statement, of the generic name *Nitella* was a mistake. A description of the plant, with diagnoses of the new genus and species that it represents, will be given in the larger publication mentioned at the close of this paragraph.

The drawings selected for illustration represent (*a*) an early four-celled stage of each of the organs involved; the account of the origin and development of which will be deferred; and (*b*) the nuclear divisions, in the apical cells of these organs and elsewhere, that are significant.

THE OOGONIUM

In figure 1 is seen a young oogonium. It is composed of the basal, stalk, and nodal cells forming the support of an apical cell which at this stage is less than a hemisphere. This cell enlarges vertically and still more transversely in becoming the ovoid primary oocyte. It soon enters meiosis, which proceeds rapidly, concurrent with the setting off by the nodal cell, in rapid succession, of the primordia of the sheath cells.

The details of the heterotype division have not yet been fully worked out. A single figure (2) is shown in the pachymena. The nucleus of the nodal cell is also seen, in a prophase of a somatic mitosis for the formation of a sheath cell primordium.

The metaphase of heterotype division is shown in figure 3. The sixteen bivalent chromosomes, spheroidal in form, and differing but little in size, are in a ring-shaped group (the equatorial plate of the earlier terminology) which has moved from the center of the cell toward its smaller end, where the polocyte is given off. In this, as in later stages of the meiosis, the spindle is indicated by elongated groups of granules, but clearly defined fibers have not been observed.

The first step beyond the metaphase is shown in figure 4. Disjunction is nearly complete in the case of six bivalents; the remaining ten, though more or less elongated, show little if any indication of separation as yet.

In figure 5 is seen the beginning of the anaphase. Eighteen distinct univalent chromosomes are seen and seven bivalents in which separation is not entirely complete, the univalents being connected by slender strands.

Figure 6 is of special interest on account of the striking coincidence shown. An early but distinct anaphase is seen in the oocyte with sixteen chromosomes in each group. Directly beneath the oocyte the nodal cell is seen in a somatic mitosis for the formation of the nucleus of a sheath primordium. The early telophase with thirty-two chromosomes in each group is shown. The significance of the contrast renders comment unnecessary.

The completion of the heterotypic division in the primary oocyte results in the formation of two nuclei of decidedly different size. The larger is that of the considerably enlarged secondary oocyte which very early enters into the homotypic division. The smaller is that of the polocyte, and its division is deferred until much later. A cell wall is soon formed around the polocyte, which remains within the wall of the parent cell.

In figure 7, the homotypic division of the nucleus of the secondary oocyte is shown in a stage between those represented in figures 4 and 5 of the heterotypic division. Its resolution was difficult, but twenty-four chromosomes could be distinguished. At least twelve small ones, representing the products of division, could be seen, two of the larger ones were constricted if not divided, and eight large ones were clearly ovoid in form. It is evidently at the transition stage between metaphase and anaphase.

A later stage in the division of the nucleus of the secondary oocyte is shown in figure 8. It is a well advanced anaphase, with sixteen chromosomes in each of the two groups, the upper of these becoming the nucleus of the mature ovum, and the lower that of the relatively large first polar body.

It will be seen that the cell has become nearly spherical in form, with a decided increase in volume. It should be noted also that the polocyte has shifted its position, passing a short distance toward the base. During this movement it later passes through the homotypic division, thus giving rise to the second and third polar bodies. It may be added here that one instance has been found in which the polocyte nucleus was dividing. It was in a distinct and rather late anaphase but the chromosomes were so small and so crowded that an accurate count was impossible, but it was unquestionably haploid. The two polar bodies thus formed continue to move downward to the base of the ovum, where they come to rest, the lower one in contact with the first polar body. The whole process described in the preceding paragraphs results, therefore, in the formation of four haploid cells, three of which (one small one, and two that are still smaller), with their own cell walls, lie upon the surface of the cytoplasm of the single, very much larger one whose wall surrounds the whole group.

THE ANTHERIDIUM

As has been previously stated, the apical cell of each of the organs involved is, at a certain stage, the uppermost of a column of four cells. Figure 1 has been chosen as a representation of this stage in one of them. Figure 8 has been selected for a double purpose. One of these is plainly indicated in the two preceding paragraphs; the other is to show, side by side, and arising from the same axial node, the two organs in question, although each of them has passed somewhat beyond the stage that is shown in figure 1.

In the one to the right, the apical cell has become the oocyte, which has nearly completed the meioses which convert it into a group of four haploid cells. In the one to the left the apical cell has enlarged and has completed the meioses which convert it also into a group of four haploid cells. Parting walls have been formed between them and it is now an antheridium in the four-celled stage. The homology of the two changes just stated is evident.

This figure shows, also, that there are some noteworthy differences between the three-celled columns of support. The most conspicuous is the position of the nodal cell, between the two others in one case, and above both of them in the other. The entire structures are, however, essentially homologous. Discussion of this matter must be deferred.

The drawings shown in the plates have in every instance been made with the cell (or cells) concerned *in place*. For this reason it has not been practicable to select for the antheridium a series in succession to the same extent as has been done in the case of the oocyte. Three drawings have been chosen, as especially significant.

In figure 9 is seen an antheridium in which the heterotypic division has taken place. The two nuclei thus formed lie side by side in the undivided mass of cytoplasm, each is in prophase for the homotypic division. In addition, attention may be drawn to the fact that the nodal activity has advanced beyond that indicated in figure 8, although the antheridium is still in the one-celled stage.

In figure 10 the antheridium is shown, as in figure 8, in the four-celled stage with 'resting' nuclei. Between it and the node is seen the cell that is of special interest. Its nucleus is seen in a late anaphase, with thirty-two chromosomes in each group, for the division that results in the formation of the nuclei of the stalk cell and the pedicel.

The antheridium shown in figure 11 (three quadrants represented) is in the eight-celled stage which results from the division of each quadrant into an outer and an inner primary cell. The nuclei of the inner primary cells are all in the resting phase. Those of the outer primary cells are all in mitosis for the division of the outer primary cells into the sheath cells and the manubria, by means of which the antheridium reaches the twelve-celled stage. The nucleus of the outer primary of the median quadrant is seen in prophase. That of the one to the left is passing out of metaphase, while that of the one to the right is in an advanced anaphase, with two groups of sixteen chromosomes each. The inner group (seen through the border of the median outer primary cell) is much more concentrated than the outer.

To the preceding statements it may be added that mitoses distinctly haploid have been seen at almost every step in the formation of the structures that fill the interior of the fully developed antheridium, from the division of the inner primary cells to form the single capitulum and capitellum in each quadrant to those of the cells in the spermatic filaments. Mitoses, certainly diploid, have been seen in cells as variously located in the somatic structures.

SUMMARY

1. In the charophyte under discussion the reduction divisions take place in the apical cells of two similar outgrowths from a somatic axis.

2. The outcome in each instance is the formation of a group of four cells, the nuclei of which have sixteen chromosomes.

3. In the case of one of the (modified) apical cells, the oocyte, the four cells are not all alike, one, the ovum, being very much larger than the others, which are the polar bodies (the well-known *Wendungszellen*). In the case of the other apical cell they are alike, becoming the quadrants of the antheridium.

4. The mitoses that take place in the quadrants, and in the succession of cells derived from them, are haploid.

5. The mitoses that take place in the plant body, formed by the germination of the fertilized ovum, are diploid.

If these propositions are in accordance with the facts, they will doubtless be accepted as justifying the statement, made in the communication to *Science*, "that the plant-body is in the diploid phase (the $2x$ — generation)."

EXPLANATION OF PLATES

The drawings were made with a camera lucida; the drawing board was in each instance placed at the proper level to give a projection of approximately 1200 diameters. They have been reduced one-half in preparing the plates. The optical combination used has been given for each of the figures except one.

The following abbreviations have been used with the figures:

a., antheridium.
a.i. anth. internodal cell.
ap.c., apical cell.
a.n., anth. node.
a.st.c., anth. stalk cell.
b.c., basal cell.
f.c., first cleavage of quadrant.
i.p.c., inner primary cell.
m.m., manubrial mitosis.
n.c., nodal cell.
o.p.c., outer primary cell.
o.st.c., oog. stalk cell.
pdcl., pedicel.
pol., polocyte
pr.o., primary oocyte.
q.c., quadrant cell.
sh.c., sheath cell.
s.o., secondary oocyte.
sup., 'supporting' cell.

PLATE 22

Fig. 1. A young oogonium. L. fl. 2 mm.:6x.

Fig. 2. Oogonium with primary oocyte and nodal 'nuclei' in action. Sp. achr. 1.9 mm:10x.

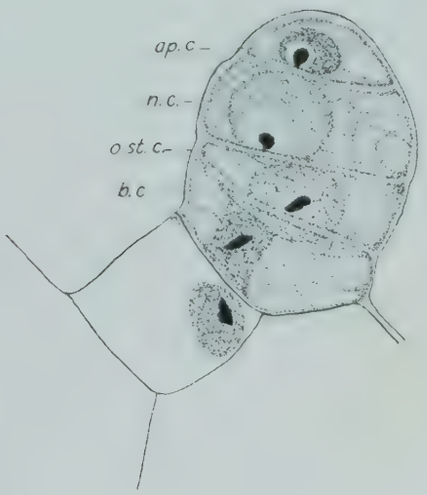
Fig. 3. Oocyte nucleus in heterotype metaphase. L. fl. 2 mm.:10x.

Fig. 4. Oocyte nucleus passing out of metaphase (heterotypic). The combination used was not recorded.

Fig. 5. Oocyte nucleus in early anaphase. L. fl. 2 mm.:10x.

Fig. 6. Oocyte nucleus in anaphase: nucleus of the nodal cell in mitosis (anaphase). Z. apo. 2 mm.:10x.

Fig. 7. Secondary oocyte, with polocyte, the nucleus of the oocyte passing out of metaphase (homotypic). L. fl. 2 mm.:6x.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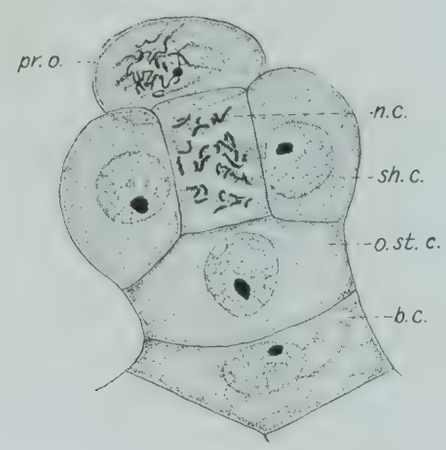
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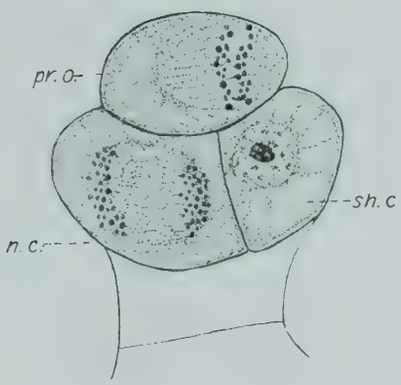
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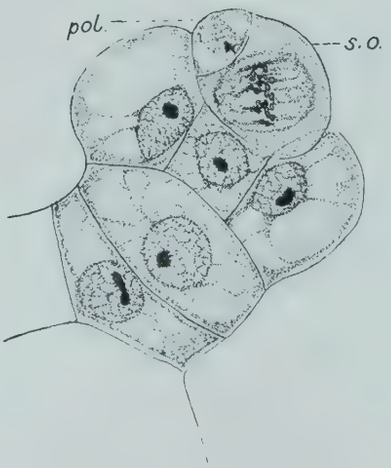
pol.
s. o.

PLATE 23

Fig. 8. Antheridium and oocyte with their supporting structures, arising side by side upon an axial node; the oocyte nucleus in anaphase for the formation of the first polar body. L. fl. 2 mm.:6x.

Fig. 9. Antheridium in one-celled stage with two nuclei in homotypic prophase. Z. apo. 2 mm.:10x.

Fig. 10. Antheridium in four-celled stage (quadrants). The 'supporting' cell beneath it is in the anaphase of a somatic mitosis. Z. apo. 2 mm.:10x.

Fig. 11. Antheridium in eight-celled stage; three quadrants are shown with the nuclei of the outer primary cells in mitosis. Z. apo. 2 mm.:10x.

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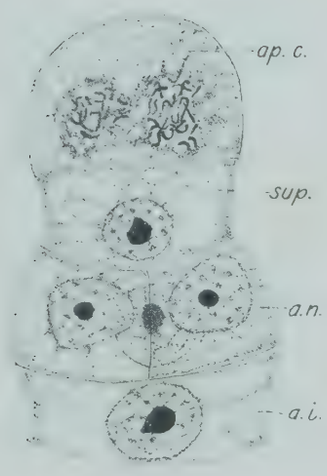
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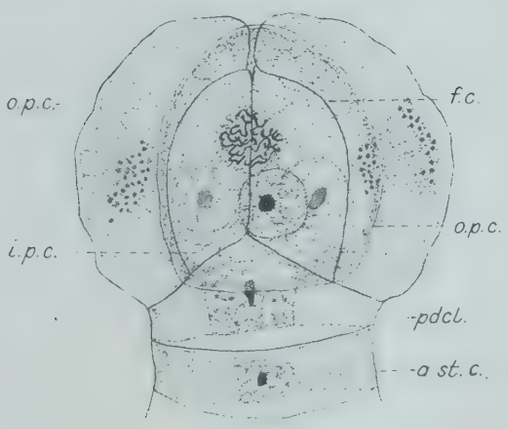
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NEW RHODOPHYCEAE FROM THE PACIFIC COAST OF NORTH AMERICA. II

BY

NATHANIEL LYON GARDNER

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NEW RHODOPHYCEAE FROM THE PACIFIC COAST OF NORTH AMERICA. II

BY

NATHANIEL LYON GARDNER

Bangia maxima sp. nov.

Fronds attached by a basal disk at first, later, in addition, by intramatrical rhizoids springing from 50 to 70 cells, cylindrical and solid in the juvenile state, becoming irregularly clavate and hollow in the terminal mature parts, 15–20 cm. (up to 35 cm.) high, 60–70μ (up to 100μ) diam. in the monosiphonous basal part, up to 6 mm. diam. at the apices; cells purple in color, 3–5 times shorter than their diameter in the monosiphonous parts, with thin, opalescent cell walls in the older parts, the outer walls common to all of the cells 15–25μ thick; antheridial membrane surrounding the cavity up to 100μ thick; antheridial groups complex and very variable in shape and size, narrow or wider and cylindrical or conical, tapering toward the interior.

Growing on boulders in the middle littoral belt at the mouth of Bolinas Bay, Marin County, California. Type, Gardner, no. 4581 (Herb. Univ. Calif. no. 284058).

This is the largest species of Bangia that has been discovered. It has been found but once, and then in great abundance, in the above mentioned habitat. I have searched in vain in the region in the immediate vicinity of the type locality but no trace of other specimens has been located and the rocks upon which the type was found have since been completely covered many feet deep by the shifting sand. It is closely related to *B. vermicularis* Harvey. The color, the shape of the vegetative cells below, and the abundance of intramatrical rhizoids resemble those characters in Harvey's species. The plants, however, are not so much contorted as in that species and are very much larger. In the outer cavernous portion, up to 6 mm. in diameter, the cavity is surrounded by a membrane which in antheridial fruit is about 100μ in diameter.

Bangia tenuis comb. nov.

Filaments free-floating, 4–8 mm. long, 16–20μ diam., cylindrical; cells mostly quadrate, in part slightly longer or shorter, more or less spherical in the apical older parts; reproduction unknown.

Bangia atropurpurea forma *tenuis* Collins, *in* Collins, Holden, and Setchell, Phyc. Bor.-Amer. (Exsicc.), no. 1341 (***nomen nudum***).

Floating among other filamentous algae in a salt-water pond on the north side of Orcas Island, opposite East Sound, Washington.

No additional information has been obtained concerning this collection since its discovery. In its present state, it seems quite definitely not a form of *B. "atropurpurea"* or *B. fuscopurpurea*. The filaments are much too slender and the cells are of a different form from those of the above mentioned species, even in young condition. It is to be regretted that we have not been able to find the fruiting condition to give us the complete life-cycle.

Erythrotrichia Kylinii sp. nov.

Filaments monosiphonous below, composed of two or more series of cells above, 1–2 mm. high, 25–35μ diam., attached by short, rhizoidal filaments from the basal cell; cells 0.5–1 times as long as the diameter; chromatophore band-shaped.

Epiphytic on other algae in the lower littoral and upper sublittoral belts. St. Paul, Kadiak Island, Alaska, to Puget Sound, Washington. Type locality in the vicinity of Friday Harbor, Washington. *Erythrotrichia Bertholdii* Kylin, Mar. Red Alg., 1925, p. 8, fig. 2, *a-e* (*non* Batters, 1900, p. 375. *Erythrotrichia ceramicola*, Setchell and Gardner, Alg. N.W. Amer., 1903, p. 292. (*non* [Lyngb.] Aresch., 1850, p. 210.)

Kylin (*loc. cit.*) remarks that he hesitatingly refers certain collections of *Erythrotrichia* made in the vicinity of Friday Harbor, Washington, to the little known *E. Bertholdii* of Batters. The writer has not seen any of the same material figured and described by Kylin nor any of the material described by Batters but has seen material on various occasions collected in the same general region as that collected by Kylin and seemingly of the same species. Judging from a study of this material and from the brief description and excellent figures produced by Kylin, the writer is led to conclude that our west American material is entirely distinct from the European material

as described by Batters. The filaments of *E. Bertholdii* are clavate, 10–12μ diameter at the base, gradually increasing up to 60–70μ in the widest part. The particularly distinctive character is the radial arrangement of the cells as seen in cross-section in the widest portion of the filaments. This arrangement of cells has not been reported in any material within our territory.

I am including the material reported from St. Paul, Kadiak Island, within this species with doubt. The material is epiphytic on a species of *Lophosiphonia* and is young, the filaments being only a small fraction of a millimeter long for the most part. They are just beginning to show formation of asexual spores. More study will be required to settle definitely the systematic postion of this northern material. It differs from *E. ceramicola* (Lyngb.) Aresch., as illustrated by Thuret, 1863, pl. 3, fig. 1, and from *E. carnea* (Dillw.) J. Ag., synonymous with *E. ceramicola* according to J. Agardh, as illustrated by Rosenwinge, 1909, p. 68, in having a band-shaped chromatophore instead of a star-shaped one, as shown in the illustration.

Erythrotrichia porphyroides sp. nov.

Plate 24, figures 4, 5

Fronds attached by a more or less expanded basal cell, or in age with a few short rhizoidal filaments, up to 2 mm. high, remaining monosiphonous until attaining a large portion of its length, then becoming ribbon-like by longitudinal as well as horizontal divisions of the cells. The meristematic regions are numerous in the frond, producing a very irregular outline. In places they are 6–8 cells wide while near by parts remain monosiphonous, at length attaining a width of 12–16 cells or over 100μ; cells quadrate, with rounded angles; chromatophores band-shaped.

Growing on *Laminaria Sinclairii* (Harvey) Farlow, Fort Point, San Francisco, California. Type, Gardner, no. 3419. June.

Erythrotrichia porphyroides in its mature condition resembles to a considerable extent the early stages in the development of certain species of *Porphyra*. One of the distinguishing characters is the irregular growth in different parts of the frond. At times the divisions of cells resulting in width of the frond take place in a plane 90 degrees opposite to that in which the normal divisions take place, resulting in irregular expansions of the frond. The plants thus far examined are scarcely mature, little having been learned of the reproductive cells.

Erythrotrichia pulvinata sp. nov.

Plate 24, figures 1, 2, 3

Erect fronds arising from a small, at first flattened, later almost spherical, cushion-shaped base; monosiphonous when young and throughout life in lower parts, soon becoming polysiphonous above by longitudinal divisions of the cells, remaining band-shaped and gradually increasing in width up to 8 cells toward the apices, but remaining 1 cell thick; basal layer, or cushion, starts from a single cell and by divisions soon establishes radiating, creeping filaments, finally completely coalescing; later the cells in the center of the cushion begin to elongate perpendicular to the surface and divide several times radially, building up a more or less spherical cushion with a single layer of peripheral protoplasts, the center being composed of gelatinous cell walls; cells of the erect filaments mostly quadrate but at times slightly longer or shorter than the diameter, arranged fairly regularly in longitudinal and cross rows; diameter of filaments below, 15–18μ, the outer flattened portion up to 60μ wide; chromatophore band-shaped, unbroken when young.

Epiphytic on the apices of the utricles of *Codium fragile* and on *Chondrus* sp. Central California (Carmel Bay). Type, Gardner, no. 2896, Pebble Beach, Carmel Bay. May.

So far as the observations have extended, this species of *Erythrotrichia* is confined exclusively to the above-named hosts. It has not been possible as yet to ascertain whether or not the basal cushion ever functions in reproduction, as Howe (1914, p. 77) has shown for the basal disk of *E. polymorpha*. There is a great deal of variation in the number and the time of origin of the erect filaments. In some cases a relatively large, almost spherical cushion appears without any erect filaments present. Again, several well developed filaments are present on very small, apparently young cushions. Specimens have been observed with as many as sixty erect filaments but usually there are only fifteen to twenty from a single base. These arise more generally from the marginal region of the cushion instead of the center where the longest cells exist. Before the erect filaments develop, the cells of the young or almost mature basal disk resemble in color and general form certain compact groups of cells of the Chamaesiphonaceae; e.g., *Dermocarpa*. Reproduction not observed.

Erythrotrichia Parksii sp. nov.

Filaments attached by short rhizoids from the basal cell, densely caespitose, pinkish purple in mass, 8–12 cm. long, 15–18μ diam., nearly uniform in diameter throughout the entire length; cells quadrate to slightly longer or shorter; chromatophores band-shaped.

Growing on other species of Algae, Eureka, Humboldt Bay, California. Type, Parks, no. 1659 (Herb. Univ. Calif. no. 276346). Eureka. May.

The material of this species appears to be immature, many of the filaments not showing any indication of fruiting. The older parts of many of the filaments show monospore formation. The length of the filaments is far greater than that of any other described species of the genus. On drying, the material has a distinctly purple hue. In dimensions of the cells, character of the chromatophores and of the monospore formation, the species shows a close affinity to *Erythrotrichia Kylinii* of this paper.

Erythrotrichia Parksii var. **minor** var. nov.

Plate 24, figures 6, 7

Fronds attached by irregular rhizoids from the basal cell, 4–8 mm. high, 16–20μ diam., varying but little in diameter throughout the entire length, pink in color; monospores and female gametes in the same filaments.

Epiphytic on *Cryptosiphonia,* in the lower littoral and upper sublittoral belts. Known from only a single locality, viz., Neah Bay, Washington. Type, Gardner, no. 3869. May.

If the methods of reproduction previously observed and described by various writers have been correctly interpreted, this species has both asexual and sexual methods represented in the same individual filaments. Scattered indiscriminately in the same filament are the so-called monospores and female gametes with their protoplasmic prolongations extending beyond the surface of the original cell walls and at times having attached small cells, seemingly the male gametes. These latter gametes were not observed in the filaments of *E. Parksii,* possibly owing to differences in age. Aside from this difference, the greatest disparity between the species and the variety is represented in the size.

Erythrotrichia tetraseriata sp. nov.

Fronds attached by the basal cell alone or in addition by short rhizoids from the basal cell, .5–1.5 cm. long, monosiphonous for some time, becoming quadrasiphonous eventually in the outer portion by two successive longitudinal cell divisions; monosiphonous portion 18–25μ diam., mature fruiting ends 38–44μ diam.; cells quadrate to slightly longer than the diameter, a few cells at base 2–4 times as long as broad; chromatophores band-shaped, entire or at times split lengthwise.

Epiphytic on *Zostera*, San Pedro, California. Type material Collins, Holden, and Setchell, Phyc. Bor.-Amer. (Exsicc.) no. 782, sub. *Erythrotrichia investiens*.

I have not been able to examine the type or any authentic material of *Erythrotrichia investiens*, but judging from the all too meager original description and figures, our plant belongs to a different entity, being larger in all of its dimensions, remaining cylindrical, and having four rows of cells.

Cryptopleura corallinara (Nott) comb. nov.

Acrosorium corallinarum (Nott) Kylin, Studien ueber Deless., 1924, p. 78. *Nitophyllum corallinarum* Nott, Nito. of Calif., 1900, p. 24, pl. 3, fig. 10; Collins, Holden, and Setchell, Phyc. Bor.-Amer. (Exsicc.) no. 2246d (sub *Nitophyllum violaceum*).

When Nott proposed *Nitophyllum corallinarum* (*loc. cit.*) he had but very scanty and imperfect material at his disposal upon which to base his description. Since then a plentiful number of specimens from different localities in southern California has been assembled, representing all the forms of reproductive organs. Careful study of this material leads to the desirability of keeping up the species to include very small forms with abundant, narrow, creeping fronds, giving rise to more or less abundant lateral, narrow, erect fronds. The species is closely allied to *Cryptopleura crispa* Kylin. It grows on other red Algae, especially on members of the Corallinaceae, and on various species of *Gelidium* and *Prionitis*. The color and structure of the fronds, the highly developed, prostrate attaching portion, and the position of the tetrasporic sori in small marginal proliferations on both the prostrate and the erect parts of the frond are characters linking this species to *Cryptopleura* rather than to either the genus *Acrosorium* or the genus *Nitophyllum* as outlined by Kylin (1924).

Cryptopleura spatulata sp. nov.

Plate 27

Fronds flabellate, repeatedly and subdichotomously branched. 14–20 cm. high, 1–1.5 cm. wide, thin and papery; the segments cuneate below, terminal segments broader and rounded, monostromatic above, composed of three layers of cells for the most part below; macroscopic veins absent or only very indistinct below; microscopic veinlets throughout the fronds; tetrasporangia born in sori on distinct, stipitate, marginal proliferations; procarps and antheridia unknown; color, rose pink.

Cast up from the sublittoral belt. (?) Southern California (San Pedro and Santa Barbara). Type specimen Mrs. H. P. Johnston, no. 256 (Herb. Univ. Calif. no. 94833). San Pedro. August.

This species of *cryptopleura* is probably closely related to *C. lobulifera* (J. Ag.) Kylin, the type locality of which is Pacific Grove, California. It has no indication of a midrib, and the veins are only slightly visible in the lower parts. It differs from *C. lobulifera* in being much thinner throughout, more fragile, and of a different color. The fruit, so far as is known, is developed exclusively on distinct marginal proliferations. It appears to be very rarely cast ashore, if indeed it grows in the sublittoral belt.

Plate 27 is a photograph of the type specimen dried.

Cryptopleura brevis sp. nov.

Plate 25, figure 2. Plate 26, figures 1, 2

Fronds with flattened, creeping, basal attachments, 7–10 cm. high, 8–15 mm. wide, flabellate, subdichotomously branched; segments linear or in part somewhat wider and rounded above, more or less strict but usually with rounded angles; macroscopic veins very distinct below, repeatedly forking and anastomosing, finally vanishing into microscopic veinlets above; tetrasporangia in sori on sessile, marginal outgrowth extending around the apices of the segments; cystocarps on similar special outgrowths or on the main body of the segments; antheridia on very much crenulated margins; color, dark purplish violet.

Growing on rocks or on other algae, in the lower littoral belt, exposed to the surf. Central California. Type, Gardner, no. 6188. (Herb. Univ. Calif. no. 284071), Moss Beach, San Mateo County, California. October.

This species of *Cryptopleura* is a near relative of *C. violacea* (J. Ag.) Kylin. Plate 25, figure 2, represents a tetrasporic plant and plate 26, figures 1 and 2, represent, respectively, cystocarpic and antheridial plants.

Cryptopleura dichotoma sp. nov.

Plate 25, figure 1

Fronds diminutive, 2–2.5 cm. high, about 1 mm. wide, regularly and dichotomously branched, the distance between the forkings usually equal to the width of the segments, with widely divaricate segments and blunt apices; ecostate; macroscopic veins absent; microscopic veins sparse but distinct, at times extending to the margin of the growing point; segments with smooth, entire margins; reproduction unknown; color, light, pink.

Habitat unknown, presumably in the sublittoral belt. San Pedro, California, the type and only known locality. Type, Mrs. H. P. Johnston, no. 237 (Herb. Univ. Calif. no. 94866).

Cryptopleura dichotoma is the most diminutive species of the genus that has yet been proposed. The lack of any kind of reproductive organs makes its generic position very uncertain. Its anatomy and its gross morphological characters ally it with the genus *Cryptopleura* in which it may remain for further study. The illustration (*loc. cit.*) is of the only known specimen. Plate 25, figure 1, represents this specimen, natural size, dried.

Hymenena Kylinii sp. nov.

Plate 32, figures 1, 2, 3

Fronds erect and rigid, 8–10 cm. (up to 20 cm.) high, 5–8 mm. wide, dichotomously or subdichotomously and sparsely branched, with linear segments, blunt apices, and smooth margins; usually much contorted, and the antheridial plants more or less crisped, attached by flattened, branched outgrowths at the base, short stipitate; midrib becoming the stipe below, branching into the segments above and vanishing before reaching the apices; microscopic veinlets absent or rare; cystocarps distributed over the segments without order; antheridia confined more generally in irregular sori near the apices and along the margins; tetrasporangia arranged in narrow, longitudinal or in part flabellar, anastomosing sori.

Growing on rocks exposed to heavy surf in the lower littoral belt, central California. Type locality, Lands End, San Francisco.

Nitophyllum Harveyanum Nott, Nito. of Calif., 1900, p. 29 (not of J. Ag.). Collins, Holden, and Setchell, Phyc. Bor.-Amer. (Exsicc.) no. 693.

Kylin (1924, p. 83), in discussing *Hymenena flabelligera* (J. Ag.) Kylin, remarks that there are two specimens in J. G. Agardh's herbarium under the name of *Nitophyllum flabelligerum* J. Ag., collected by Berggren in the Golden Gate, California. In figure 68 (*loc. cit.*) he presents an illustration of these two specimens, one of which is several times larger than the other. He considers the larger of these as the type of Agardh's *N. flabelligerum* and likens the other to the plants distributed in the Phycotheca Boreali Americana, no. 693 (under *N. Harveyanum*), cited above. It is his opinion that the plants of this distribution, which are from the type locality of the above mentioned plants in Agardh's herbarium, are not identical with the material of *N. Harveyanum* from "Australia." On page 81 (*loc. cit.*), in discussing *N. Harveyanum* J. Ag., Kylin states that the type specimen of this species is in Agardh's herbarium, that it is a tetrasporic plant, and that the tetrasporic sori are distributed over the middle parts of the frond. Figure 65 (*loc. cit.*) represents this type specimen. The illustration shows it to be very different in general form from our plant and, as suggested by Kylin, it belongs to an undescribed species. I am here dedicating the species to him. Its nearest known relative would seem to be *Hymenena flabelligera* (J. Ag.) Kylin. The most striking resemblance between these two species is the flabellate arrangement of the tetrasporic sori. *N. Kylinii* is very much smaller and less complex in branching than *H. flabelligera* and different in general habit, the former being much more rigid and contorted.

Hymenena cuneata sp. nov.

Plate 33, figures 1, 2

Fronds 7–10 cm. high, palmately divided into few to many more or less linear lobes rounded at the apices, extending nearly to the center and there forming a decidedly cuneate base; or at times the ultimate lobes unite below, forming primary lobes from the short cuneate base; midrib very indistinct at the base, soon completely vanishing upward; macroscopic veins absent, microscopic veinlets very sparse and indistinct; cystocarps relatively sparse, scattered over the upper half of the fronds; carpospores single on the ends of the gonimoblastic filaments; tetrasporangia collected into very numerous, small, rounded sori or in part slightly elongated in the longitudinal direction of the frond and covering nearly the whole of both of its surfaces; antheridia unknown; color, dark red.

Growing on other algae in the sublittoral belt. Bering Sea. Type locality, Bering Island. Type specimens in Herb. Univ. Calif. nos. 94810, 94811.

Nitophyllum ruthenicum Setchell, Alg. Prib. Is., 1899, p. 594; Setchell and Gardner, Alg. N.W. Amer., 1903, p. 320. (Both as to material only from St. Paul Island, Alaska, collected by Mr. White.)

The character of the procarps has not been investigated but in all other respects the characters align this species perfectly with the genus *Hymenena*.

The cystocarps are conspicuous although not very abundant, and have numerous large carpospores born singly on the ends of the gonimoblasts. The microscopic veinlets are present but not numerous. The tetrasporangial sori are relatively small and very numerous, occupying the larger parts of the fronds on both sides and extending to the apices. The antheridial plants are not represented in our collections at the University of California. The type specimens are figured on plate 33. They were contributed to the herbarium of the University of California by Kjellman and labeled in his handwriting (as identified by Dr. Carl Skottsberg) *Nitophyllum ruthenicum*. Kylin (1925, p. 67) states that he has examined the type specimen of *Nitophyllum ruthenicum* (Post and Rupr.) Kjellm. and finds that it belongs to his genus *Myriogramme*, to which he then referred it, because of the absence of microscopic veins and the presence of carpospores in chains. Thus the species here described belongs to an entirely different entity notwithstanding the fact that both sets of plants under discussion were identified by Kjellman.

Hymenena Fryeana (Harv.) comb. nov.

Plate 35, figures 1, 2

Nitophyllum Fryeanum Harvey, Ner. Bor. Amer., Suppl., 1858, p. 81. *Nitophyllum multilobum* J. Ag. Sp. Alg., vol. 3, part 1, 1876, p. 698, *ibid.*, part 3, 1898, p. 45; Farlow, Alg. new to U. S., 1877, p. 238; Anderson, List, 1891, p. 224; Nott, Nito. of Calif., 1900, p. 27; Collins, Holden, and Setchell, Phyc. Bor. Amer. (Exsicc.), no. 336 (not Tilden, Amer. Alg. [Exsicc.], no. 321); (not *Hyemenena Fryeana* [Farlow] Kylin, Studien ueber Deless., 1924, p. 81, which is the *Nitophyllum Fryeanum* Farlow *in* Farlow, Anderson, and Eaton, Alg. Exsicc. Amer. Bor., no. 69, also of Gardner *in* Collins, Holden, and Setchell, Phyc. Bor.-Amer. [Exsicc.], no. 1742); *Myriogramme multiloba* (J. Ag.) Kylin (*loc. cit.*), p. 58.

From all of the evidence at hand it appears that Harvey had immature material upon which to base his *Nitophyllum Fryeanum*. The material was contributed by Mr. A. D. Frye from the Golden Gate, California. Finding the species thus imperfectly described is prob-

ably what led Agardh (*loc. cit.*) to redescribe it under the name *N. multilobum*, based upon good fruiting material, especially tetrasporic plants, very characteristic of the species, contributed from the same locality by Berggren. Later, Agardh (*loc. cit.*, p. 45) follows Farlow in applying Harvey's name to plants collected at Santa Cruz, California, and distributed in the Alg. Exsicc. Am.-Bor., no. 69. Nott (*loc. cit.*) was of the opinion that Harvey's description, imperfect as it is, more nearly suits the plants of Agardh's *Nitophyllum multilobum* than the plants distributed by Farlow (*loc. cit.*). Setchell, after having examined the material in both Harvey's and Agardh's herbaria, states in his unpublished notes that he is of the same opinion. And finally, Kylin (*loc. cit.*) has given expression to the same opinion but did not make the obvious change on the ground that the two species belong to different genera. In the same work he transfers *Nitophyllum multilobum* J. Ag. to his new genus *Myriogramme.*

I have examined abundance of fresh fruiting material and find that the gonimoblasts have "*endständigen Sporen*" instead of having the "*Sporen in ketten,*" as Kylin's diagnosis gives for Myriogramme. I am therefore removing it from that genus and placing it with the genus Hymenena as outlined by Kylin (*loc. cit.*) under the above new combination. This makes *Hymenena Fryeana* (Farlow) Kylin untenable.

Hymenena Setchellii nom. nov.

Plate 28, figures 1, 2; plates 29, 30, 31

Nitophyllum Fryeanum Farlow, 1878, *in* Farlow, Anderson, and Eaton, Alg. Exsicc. Am. Bor., no. 69, List, 1875, p. 365, List, 1876, p. 695; Anderson, List, 1891, p. 224; Howe *in* Erythea, vol. 1, 1893, p. 68; Gardner *in* Collins, Holden, and Setchell, Phyc. Bor.-Amer. (Exsicc.), no. 1742 (not *N. Fryeanum* Harvey, Ner. Bor. Amer., Suppl., 1858, p. 128; nor Tilden, Amer. Alg. [Exsicc.], no. 321). *Nitophyllum ruthenicum* Setchell and Gardner, Alg. N.W. Amer., 1903, p. 320, as to Gardner, nos. 114, 115, 226.

Growing on rocks in the sublittoral belt, Puget Sound, Washington, to central California. Type locality, Santa Cruz, California.

It seems sufficiently certain from the description of *Nitophyllum Fryeanum* Harvey (*loc. cit.*) and from the studies of Setchell on material from the coast of central California assembled in the herbaria of Farlow, Harvey, Agardh, etc., to warrant the conclusion that Harvey's plants upon which was based his description are of

the same entity as the *Nitophyllum multilobum* J. Ag. (1876, p. 698). The type locality of both species as proposed is Golden Gate, California.

Agardh later (1898, p. 45) redescribes his *N. multilobum* and compares it favorably with the plants distributed from the type locality, *in* Collins, Holden, and Setchell, Phyc. Bor.-Amer., 1897, no. 336. In the same work, p. 72, he retains Harvey's name for the plants distributed by Farlow (*loc. cit.*). Nott (*loc. cit.*, p. 23) voiced the opinion that Harvey's description better fits *N. multilobum* J. Ag. than that of *N. Fryeanum* Farlow but lacked sufficient evidence to refer the name to that plant. Kylin (1924, p. 81) states that he is in accord with Nott's opinion, but since the plants distributed by Farlow under *N. Fryeanum* (*loc. cit.*) and the plants referred by Agardh to *N. multilobum* belong to different genera (Kylin having in the same publication [*loc. cit.*] already placed Agardh's species in his new genus *Myriogramme* and Farlow's in *Hymenena*), he did not think it necessary to make a new name for the plants distributed under *N. Fryeanum* by Farlow. I have examined antheridial material from the Golden Gate, in Harvey's herbarium, under *N. Fryeanum*, and find it to be indistinguishable from antheridial material from the same locality from which *N. multilobum* J. Ag. came.

Therefore it seems necessary from all the evidence at hand that Harvey's name, *N. Fryeanum*, really should be applied to Agardh's plants under *N. multilobum*, thus throwing the latter into synonymy. This procedure leaves the plants distributed by Farlow (*loc. cit.*) from Santa Cruz and by myself from Puget Sound (*loc. cit.*) without a name, and I am proposing the new name *Hymenena Setchellii* for the entity.

The imperfect description of Harvey is undoubtedly due to the fragmentary nature of the material at his disposal. This led Agardh, who had more abundant and characteristic material to study, to describe it as a different and distinct species. The tetrasporic plants are so distinct as not to be confused with any other known species. The tetrasporangia are collected in sori arranged in transverse bands on the terminal lobes. They seem to grow more on one side than on the other, making the fronds concavo-convex.

Figure 1, plate 28, represents a cystocarpic plant and figure 2 a tetrasporic plant. These are both from dried herbarium specimens. They are deeply and narrowly lobed specimens and are a part of the same collection from Whidbey Island, Washington, distributed in the

Phycotheca Boreali Americana, no. 1742 (*loc. cit.*). Plate 29 represents a dried tetrasporic plant from Pacific Grove, California, less deeply lobed than those previously mentioned. Plate 30 represents a cystocarpic plant, much crisped and more nearly digitate, and plate 31 represents a tetrasporic plant with a few short lobes. The two last mentioned are from Whidbey Island. Aside from these representatives, there are innumerable intermediate forms. Much variation exists in other characters of the species. The plant represented on plate 29 has very conspicuous macroscopic veins at the base, while those in the plant represented on plate 31 are scarcely visible.

Gymnogongrus platyphyllus sp. nov.

Plate 24, figures 8, 9, 10, and plate 34

Fronds 18–25 cm. high, 4–6 mm. wide, distinctly flattened, with rounded margins, repeatedly and dichotomously branched, attached by a strong parenchymatous disk, at times several fronds arising from a common, apparently confluent, disk of a dark purplish red color; interior composed of large, rounded, colorless cells, 50–75μ diam. in cross-section, about two times as long as the cross diam., becoming smaller toward the surface of the frond and finally becoming spherical and giving rise to anticlinal rows (3–4 cells) of short-cylindrical, assimilating cells; reproduction unknown.

Growing attached to rocks in the lower littoral and upper sublittoral belts. Central California (Duxberry Reef, Marin County) to Lower California (Ensenada).

Type, Herb. Univ. Calif. no. 284030, Duxberry Reef, Marin County, California. *Gymnogongrus linearis* Farlow, Anderson, and Eaton, Alg. Exsicc. Am. Bor., no. 21; Howe, Mar. Alg. Peru, 1914, p. 115, as the host of *Actinococcus Chiton.*

This species of *Gymnogongrus* has been a puzzle to phycologists for many years. Specimens have never been reported with any kind of reproductive organs which have been recognized as such. The plants are relatively abundant and the writer has repeatedly examined specimens from various localities at different seasons of the year, but without ever being able to detect the slightest indication of reproductive organs. I suspect that it may reproduce by very small monospores formed on the ends of the cortical, anticlinal rows of cells.

The plants are only very rarely found, and these quite young, not inhabited by a small parasitic red alga, *Actinococcus Chiton* Howe.

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EXPLANATION OF PLATES

PLATE 24

Erythrotrichia pulvinata sp. nov.

Fig. 1. Young plants on utricles of *Codium fragile*. × 200.

Fig. 2. Young plants without erect filaments. × 200.

Fig. 3. Nearly mature plant with erect filaments. × 200.

Erythrotrichia porphyroides sp. nov.

Fig. 4. Segments of whole plant nearing maturity, showing characters of the base, apex, and other parts at different levels. × 300.

Fig. 5. A segment of a mature fruiting plant. × 300.

Erythrotrichia Parksii var. *minor* var. nov.

Fig. 6. Basal portion. × 250.

Fig. 7. Upper parts of filament. × 250.

Gymnogongrus platyphyllus sp. nov.

Fig. 8. View of cross-section, semidiagrammatic.

Fig. 9. View of the edge of cross-section. × 100.

Fig. 10. View of longitudinal section perpendicular to the flat surface of the frond. × 100.

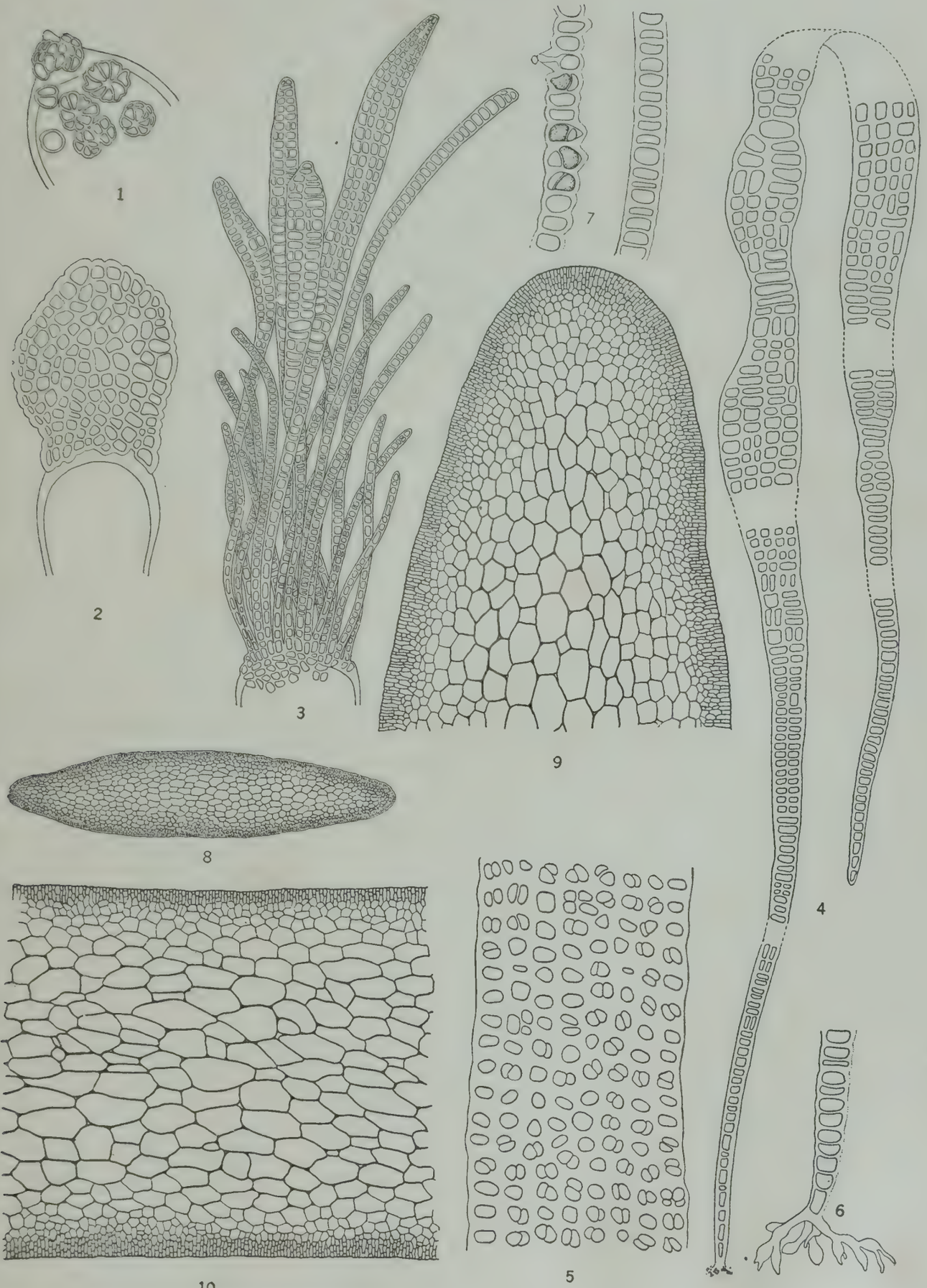
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PLATE 25

Fig. 1. *Cryptopleura dichotoma* sp. nov. Photograph of dried herbarium specimen. × 1.

Fig. 2. *Cryptopleura brevis* sp. nov. Photograph of living material with tetraspores. × 1.

Fig. 1

Fig. 2

PLATE 26

Fig. 1. *Cryptopleura brevis* sp. nov. Photograph of living material, with cystocarps. × 1.

Fig. 2. *Cryptopleura brevis* sp. nov. Photograph of living material, with antheridia. × 1.

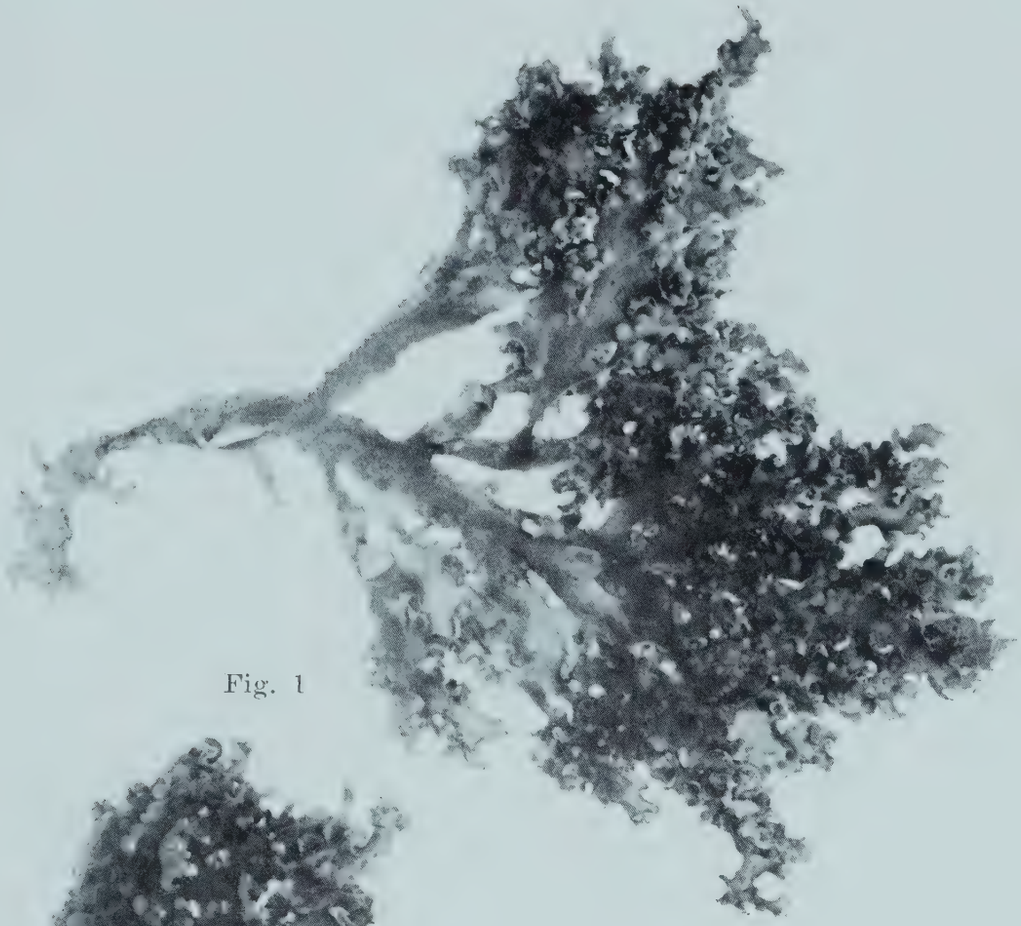

Fig. 1

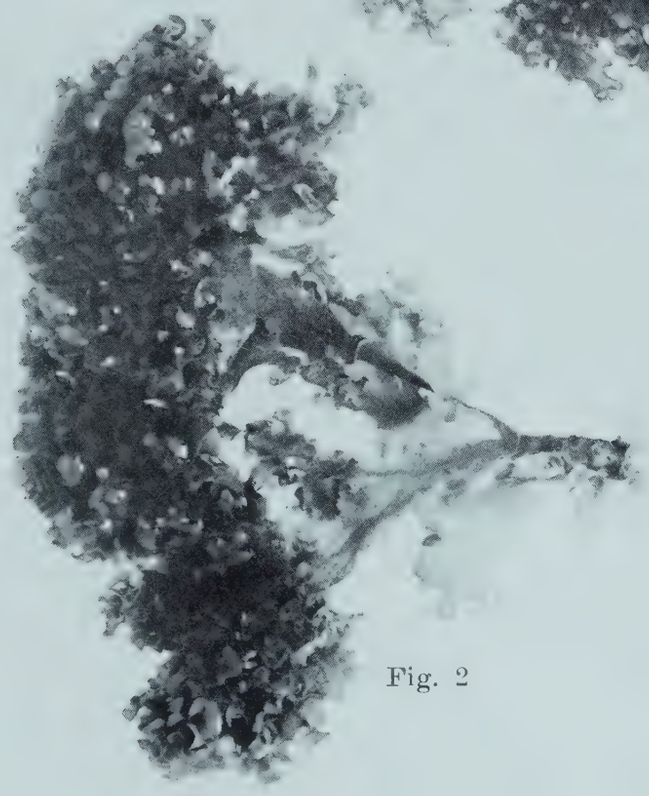

Fig. 2

PLATE 27

Cryptopleura spatulata sp. nov. Photograph of dried herbarium specimen.

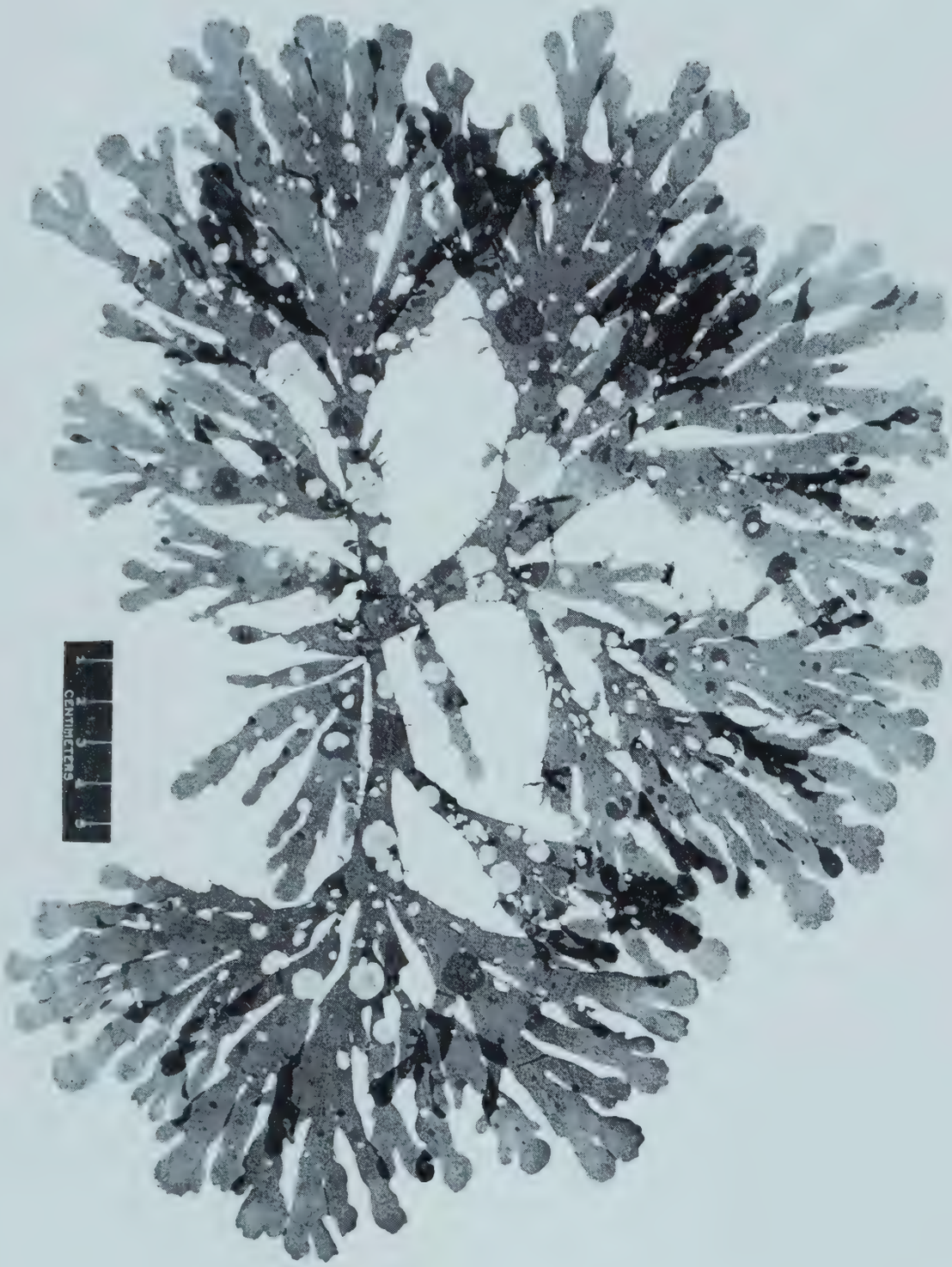
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PLATE 28

Fig. 1. *Hymenena Setchellii* nom. nov. Photograph of dried herbarium specimen, cystocarpic. × 1.

Fig. 2. *Hymenena Setchellii* nom. nov. Photograph of dried herbarium specimen, tetrasporic. × 1.

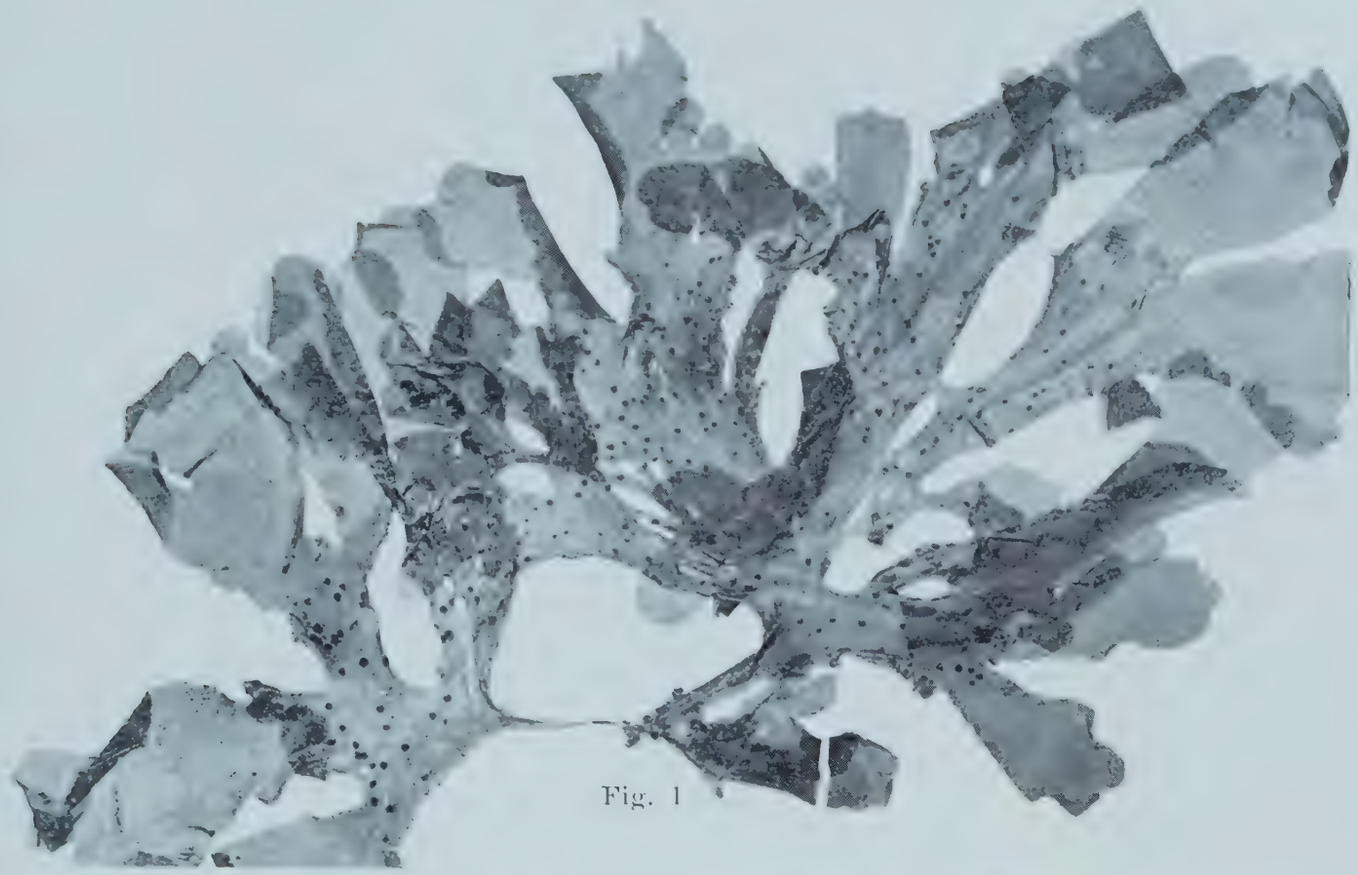


Fig. 1

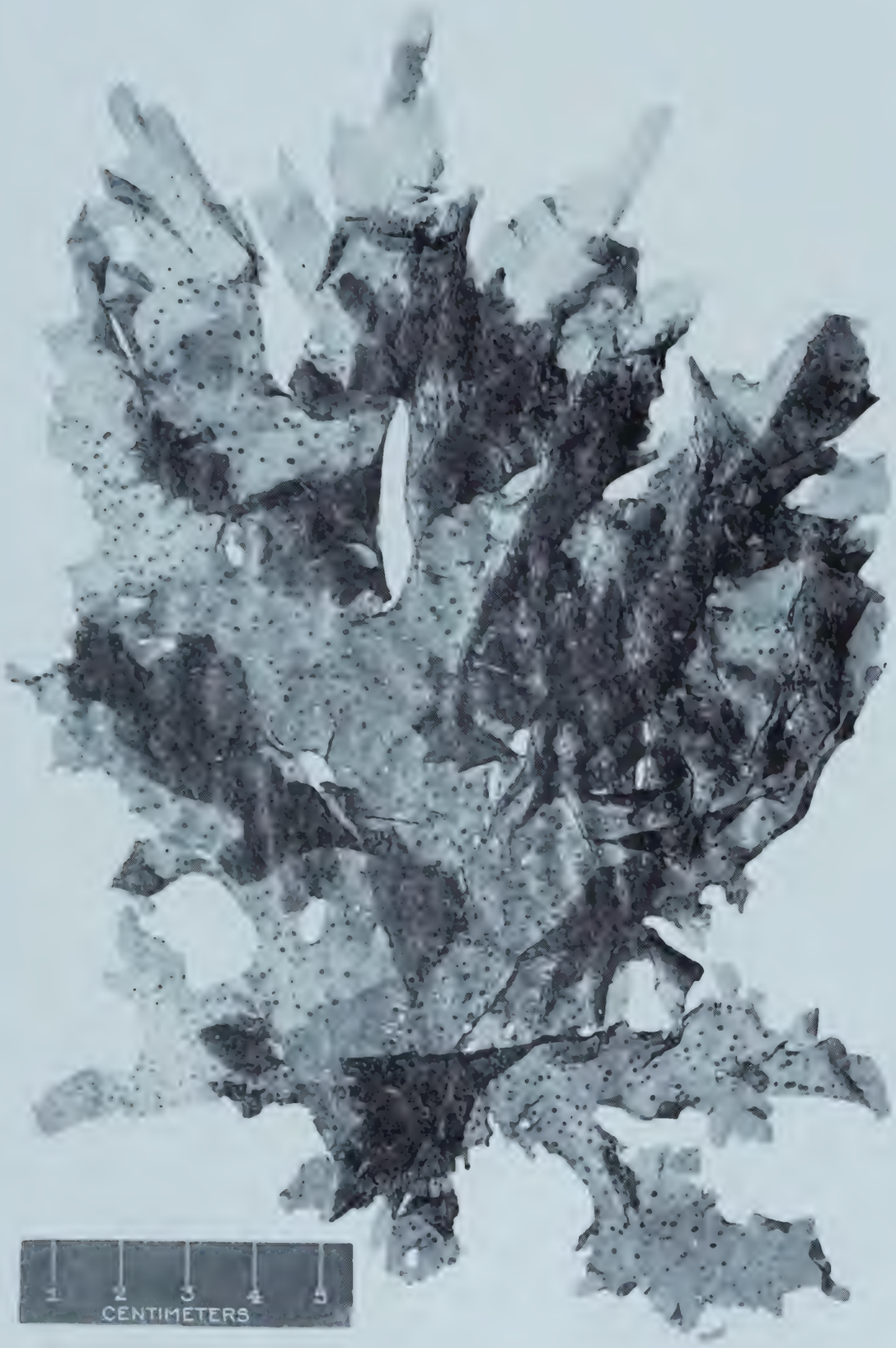
Fig. 2

PLATE 29

Hymenena Setchellii nom. nov. Photograph of dried herbarium specimen, tetrasporic. × 1.

PLATE 30

Hymenena Setchellii nom. nov. Photograph of dried herbarium specimen, cystocarpic. × 1.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CENTIMETERS

PLATE 31

Hymenena Setchellii nom. nov. Photograph of dried herbarium specimen. tetrasporic. × 1.

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CENTIMETERS
3
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PLATE 32

Hymenena Kylinii sp. nov.

Figs. 1, 2, 3. Cystocarpic, tetrasporic, and antheridial plants, respectively. Photograph of living material. × 1.

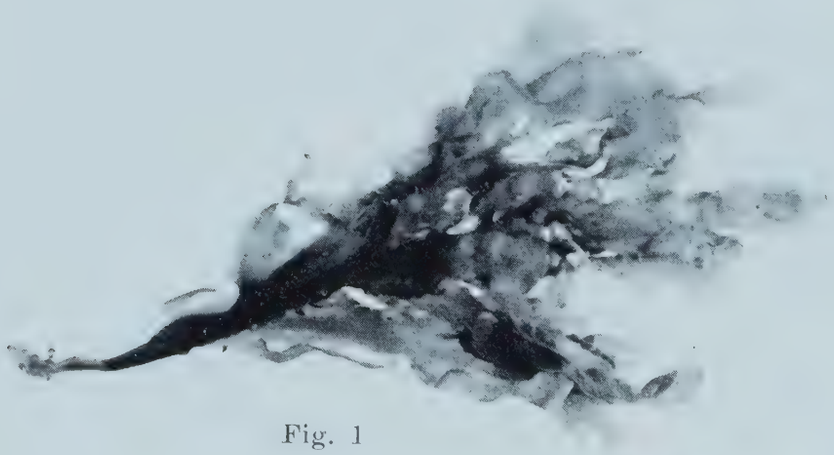

Fig. 1

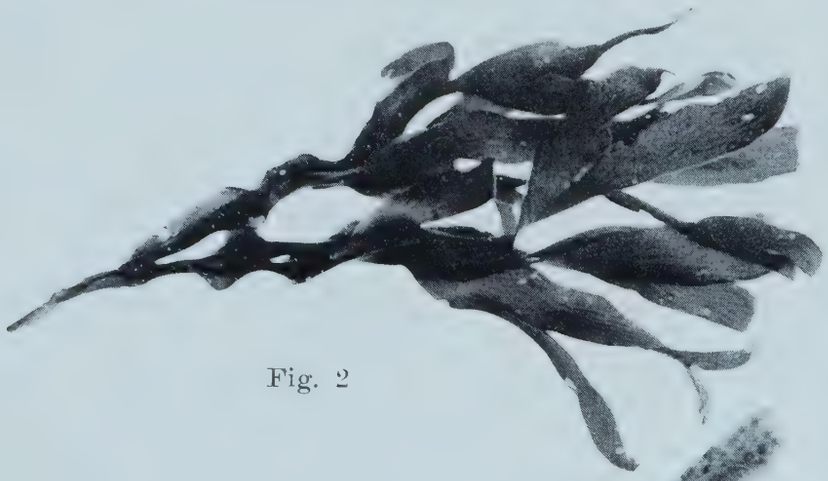

Fig. 2

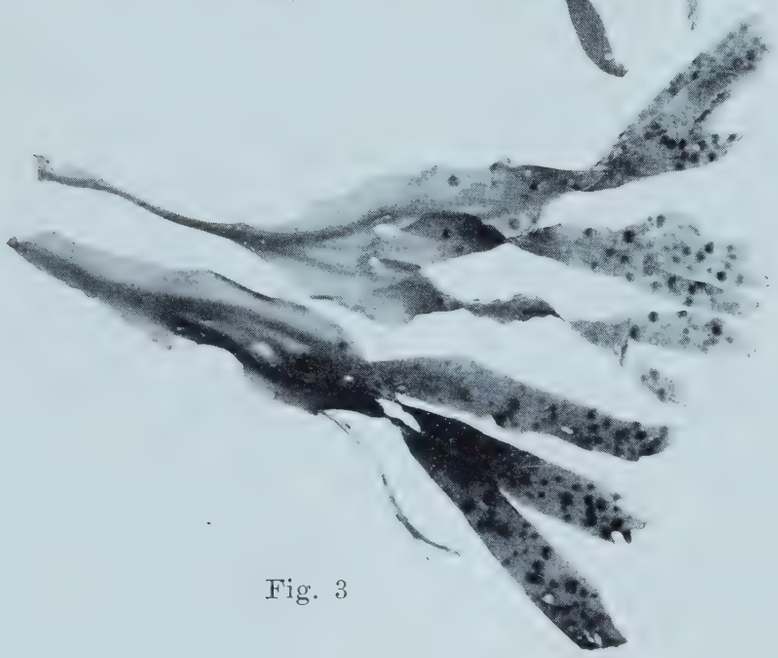

Fig. 3

PLATE 33

Hymenena cuneata sp. nov.

Figs. 1, 2. Tetrasporic and cystocarpic plants, respectively. Photograph of dried herbarium specimens. × 1.

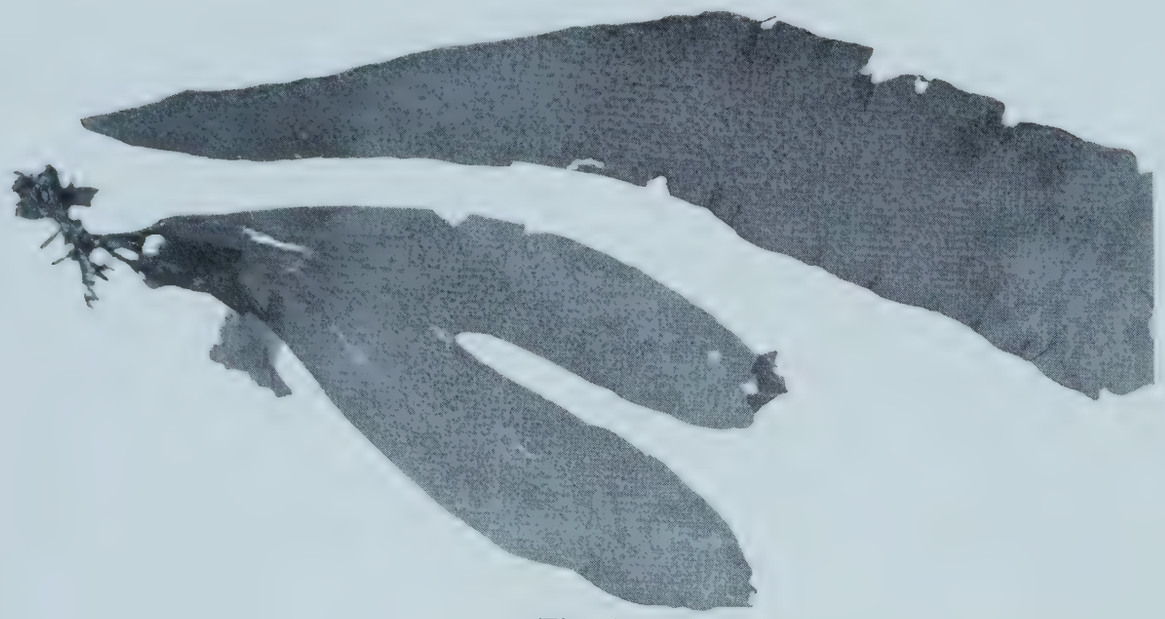

Fig. 1

Fig. 2

PLATE 34

Gymnogongrus platyphyllus sp. nov. Photograph of living material. × 1.

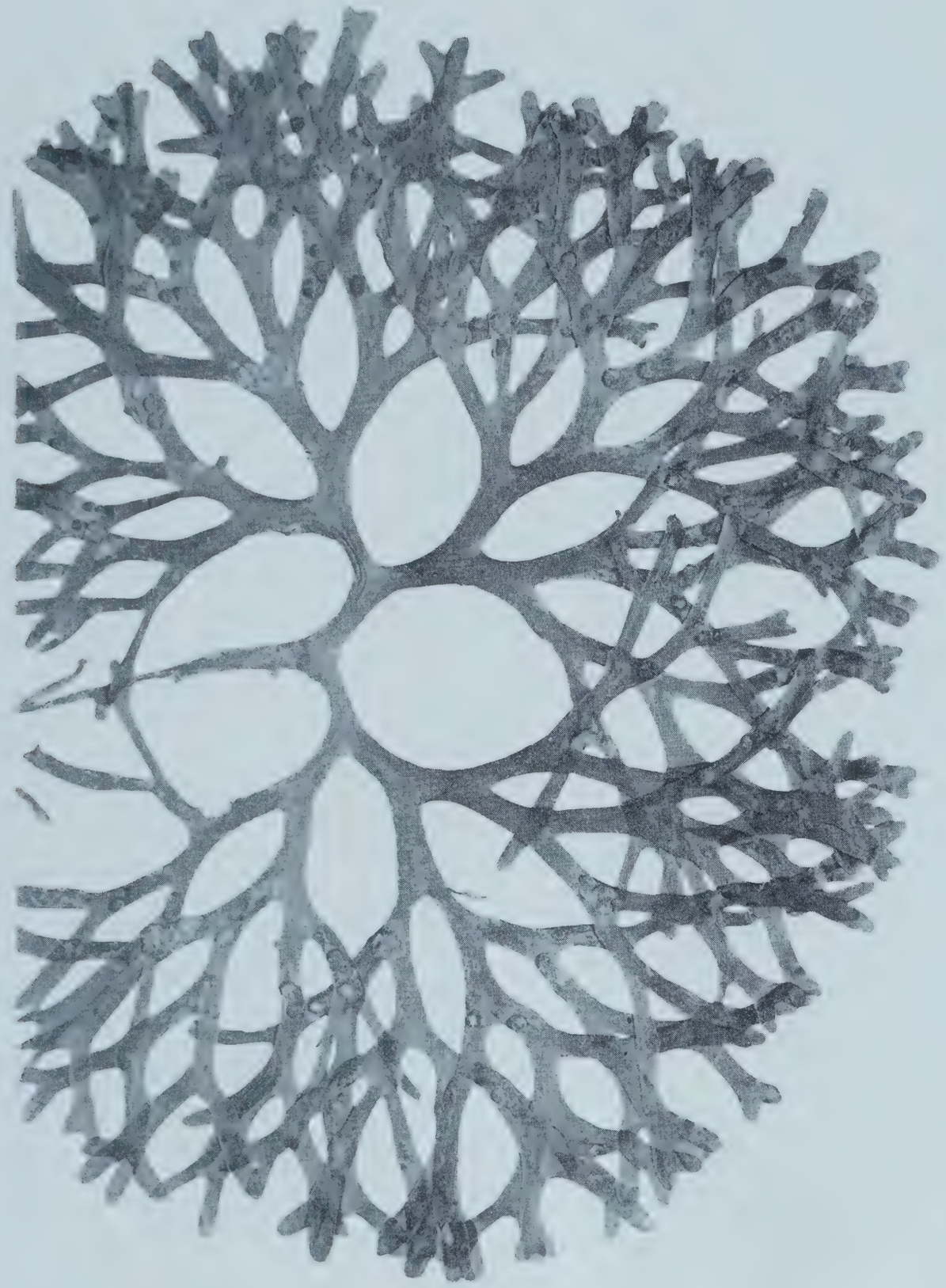

PLATE 35

Hymenena Fryeana comb. nov.

Figs. 1, 2. Tetrasporic and cystocarpic plants, respectively. Photographs of living material. × 1.

Fig. 1

Fig. 2

NEW SPECIES OF GELIDIUM ON THE PACIFIC COAST OF NORTH AMERICA

BY

NATHANIEL LYON GARDNER

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NEW SPECIES OF GELIDIUM ON THE PACIFIC COAST OF NORTH AMERICA

BY

NATHANIEL LYON GARDNER

Gelidium pyramidale sp. nov.

Plates 36 and 45; plate 37, figure 1; plate 46, figure 2

Fronds 10–16 (up to 22) cm. high, complanate, about 1 mm. wide, main fronds tapering in width only very gradually; branching alternate or opposite, distichous, of 3 orders, the ultimate and subultimate ramuli linear, very blunt; all branches constricted suddenly at their bases to about one-half their width above; surface cells as seen in surface view lenticular in form, arranged more or less in rows extending lengthwise of the fronds, about twice as long as broad; color dark red; cystocarps unknown; tetrasporangia in distinct sori in the older secondary branches and in the ultimate ramuli.

Growing on rocks in the upper sublittoral belt. Southern California. Type locality, La Jolla. Type, Herb. Univ. Calif. no. 77876.

Gelidium Amansii Collins, Holden and Setchell, Phyc. Bor.-Amer. (Exsicc.) no. 585; Collins, N. A. Algae (Exsicc.) no. 161.

Gelidium pyramidale is based upon the material from La Jolla distributed in the Phycotheca Boreali Americana (*loc. cit.*). A specimen of this collection has been designated as the type.

It is indeed perplexing to attempt to decide how to interpret *Gelidium Amansii* Lamouroux. The original description of *Fucus Amansii* Lamouroux in Dissertationes, 1805, p. 48, pl. 26, figs. 2–5, is very brief and insufficient. In the illustrations the plant seems to be cylindrical, very irregularly branched, with acute terminal ramuli. In this connection Lamouroux remarks in regard to the distribution of the species, "Habitat in insular Franciae et Madagascar oris." When Lamouroux established the genus *Gelidium* (1813) he transferred *F. Amansii* to it, but without further comment. Kuetzing published a brief description of *Gelidium Amansii* in his Species Algarum, p. 766, referring to the localities cited by Lamouroux. In Tabulae Phycologicae, 1868, p. 44, figs. *a–c,* he illustrated a plant based upon material collected at "Yokuhama," Japan, by Mertens. These illustrations would seem to show that the plants of the Japanese waters are quite different from those of Lamouroux, but they represent

Kuetzing's idea of the species. Okamura followed Kuetzing's concept, and in 1913 gave the most complete description yet presented and accompanied the description with elaborate drawings of material found in the Japanese waters. He did not, however, go into the histological characters of the species. Other Japanese phycologists, notably Yendo, have kept up the same name for the Japanese species used in the manufacture of agar agar. There is at present in the Herbarium of the University of California sufficient authentic material from the coast of Japan for study and comparison, and until it can be shown that this Japanese material is distinct from Lamouroux's type, I am taking it to represent the concept of *Gelidium Amansii* Lamouroux as well as that of Kuetzing.

Notwithstanding the similarity of our material under discussion in gross morphological characters, the plants are not identical in this respect and are decidedly different in anatomical characters. I am therefore proposing the name *Gelidium pyramidale* to take care of the entity, the name referring to the general shape of the outline of the frond.

Gelidium nudifrons sp. nov.

Plate 43; plate 37, figure 2

Fronds 16–24 (up to 40) cm. high, 300 to 500μ diam., broadly oval in cross-section, repeatedly branched, the different orders of branches varying only slightly in diameter; branches alternate, subdistichous, irregularly placed for the most part but relatively straight, smooth, almost devoid of branches in the older parts; surface cells irregularly placed, 3.5–4μ diam., equidiametric; cortical cells much larger; rhizoidal filaments abundant, mostly in the cortex but sparsely scattered through the medulla; cystocarps sparse, single, on short simple ultimate ramuli; antheridia unknown; tetrasporangia on short, more or less branched, ultimate fructiferous ramuli, extending to the usually cordate apices; color pink.

Growing in the sublittoral belt. Southern California to Ensenada, Lower California. Type, Gardner, no. 4994*b* (Herb. Univ. Calif. no. 264686). Ensenada, June.

This species probably grows in considerable depth of water. The few specimens which we have seen have been cast ashore. The fruit in all specimens thus far observed is sparse and scattered. If this proves to be the case with most of the plants it may be considered a good distinguishing character of the species. The species seems to be closely related to *Gelidium arborescens* of this paper, both species being characterized by the absence of short subultimate ramuli usually abundant in other species of this genus.

Gelidium purpurascens sp. nov.

Plates 38, 39

Fronds 12–20 cm. high, up to 1 mm. diam.; stipe and branches complanate, broadly elliptical in cross-section; branches beginning near the base, producing numerous long primary segments, 4–5 times pinnate, young branches geniculate and erect, later straightening and standing at about 45°, branches constricted at the base; color dark purple; cystocarps appearing first on the main fructiferous ramuli which later develop fertile lateral ramuli below and often become considerably elongated and at times branched at the apices; tetrasporangia forming sori on the swollen blunt ends of the fructiferous ramuli, which later produce fertile, lateral ramuli below but are not prolonged above; antheridia unknown.

Growing on rocks in pools in the lower littoral belt. Central California. Type, Herb. Univ. Calif. no. 93572. Moss Beach, San Mateo County, June.

This species of *Gelidium* seems related to *G. cartilagineum* var. *robustum* of this paper, especially so in regard to the method of branching. Young plants and young and fruiting parts of older plants have as a rule branches geniculate and bent upward, the outer part being almost parallel with the frond from which it arises. In height it approximates to that of *G. pulchrum* but is much thicker and differs in color.

Gelidium Setchellii sp. nov.

Plate 40, figures 1, 2

Fronds 25–35 cm. high, about three-fourths mm. diam., sparsely branched, slightly flattened at the base, cylindrical above; branches of three orders for the most part, occasionally more; primary branches long and slender, bearing numerous, short, secondary branches more or less irregularly placed, alternate, or in small part opposite, and mostly distichous; color dark red; branches of uniform diameter throughout, tapering slightly to the blunt apices and considerably at the bases; surface cells irregularly arranged, angular, with rounded corners, 4–6μ diam., slightly elongated radially in cross-section view; 2–3 layers of subcortical cells spherical and of approximately the same size as the cortical layer; most of the frond occupied by the medulla composed of cells circular in cross-section and 24–28μ diam., densely congested with coarse granules; rhizoidal filaments abundant in the subcortical and outer medullary tissues; cystocarps near the outer end of relatively long, simple ramuli; antheridia and tetrasporangia unknown.

Cast ashore from the sublittoral belt. Duxberry Reef, Marin County, California, the type and only known locality. Type, Setchell, no. 1083 (Herb. Univ. Calif. no. 93589).

Very little can at present be said of this species of *Gelidium,* on account of scarcity of material, but such as is available is quite distinct from other described species so far as descriptions enable one to judge.

Gelidium polystichum sp. nov.

Plate 41

Fronds about 20 cm. high, up to 1.5 mm. wide, with dense polystichous branching, complanate; branches of 4–5 orders, arranged primarily along the margins of the flattened fronds and opposite or alternate, but approximately half of them arising without order on either of the flattened sides, not conspicuously narrowed at the point of origin; ramuli mostly linear and blunt; tetrasporangia borne on short, ultimate, simple ramuli, extending to the much swollen, very blunt, and oftentimes cordate apices; cystocarps and antheridia unknown, color dark pink; cortical cells as seen in surface view arranged in fairly conspicuous, more or less radiating rows on the flattened sides, 3.5–4.5μ diam., much rounded; rhizoidal filaments arranged in the mature parts most abundantly in the cortical and subcortical tissues, scattered in the medulla.

Zonal distribution unknown. The single type specimen, a tetrasporic plant, was found cast ashore at White's Point, near San Pedro, California. Gardner, no. 1927 (Herb. Univ. Calif. no. 284088).

This species of *Gelidium* has the distinction of being the only one of the complanate section having branches of all orders arising normally from the flattened surfaces. It is to be hoped that specimens with cystocarps and antheridia may be discovered, that it may be ascertained whether or not these possess any unusual characters. The subultimate ramuli on the type specimen bear several short, unbranched, tetrasporiferous ramuli.

Gelidium arborescens sp. nov.

Plate 42

Fronds decidedly cartilaginous and rigid, 18–25 cm. high and up to 2 mm. diam., cylindrical to subcylindrical; branches usually of 4–5 orders, with one main central axis and with but few short, simple, fructiferous ramuli; color dark red; cells as seen in surface view arranged in more or less fairly definite longitudinal rows, thin walled, 4–5μ diam. in surface view, with rounded angles, approximately equidiametric, first layer of cortical cells about the same size as the surface cells, increasing gradually in size toward the medulla; rhizoidal filaments very numerous, located almost exclusively on the border between the cortex and the medulla; medullary cells short cylindrical, 25–35μ diam., with numerous intercellular spaces; cystocarps and antheridia unknown; tetrasporangia in sori on the much enlarged ends of short fructiferous ramuli, extending to the apices.

Growing in the sublittoral belt, from central California (Carmel Bay) to southern California. Type locality, Carmel Bay, Monterey County. Type, Herb. Univ. Calif. no. 93582, collected by W. A. Setchell, May.

Only tetrasporic specimens have been observed, and the fruit on these is sparse. This condition will doubtless be found to prevail on cystocarpic and antheridial plants, judging from the character of the sterile parts.

Gelidium crinale var. **luxurians** Collins

Plate 46, figure 1; plate 47, figure 3

Fronds fragile, 5–6.5 cm. high, 150–200μ diam., attached by short rhizoids, almost uniform in diameter throughout, broadly oval in cross-section, terminal ramuli almost cylindrical; main branches mostly of three orders, each order reduced slightly in size, chiefly distichous; branches not at all or only slightly constricted at the base, alternate or opposite; surface cells without definite arrangement, 6.5–8μ diam.; medullary cells relatively uniform in size, 14–18μ diam., thick walled, granular; rhizoidal filaments collected mostly in the center of the fronds; tetrasporangial sori mostly on slightly swollen fructiferous ramuli but not extending to the acute apices, occasionally in the fronds bearing the fructiferous ramuli, even at times in three orders of ramuli; cystocarps scattered either in the main fronds or toward the base in long, tapering, ultimate ramuli; antheridia in discontinuous sori at the base and farther out on the fructiferous ramuli; color dark red, usually fading to pink.

Growing on rocks in pools in the lower littoral belt, southern California. Collins, *in* Collins, Holden and Setchell, Phyc. Bor. Amer. (Exsicc.), no. 1138.

This form of *Gelidium crinale* seems closely related to *G. sinicola* of this paper. It differs from this species in being much more slender, less profusely and more regularly branched, has cells more nearly uniform in size as seen in cross-section, has straighter branches, and differs in color. I have examined a sterile fragment of the assumed type of *G. crinale* Turner, obtained from the Herbarium at Kew, England, by W. A. Setchell. Our material is considerably more slender, has a wider medulla, with differences in the size of the cells. The type specimen being sterile, I am unable to compare fruits. The illustrations cited above are of young tetrasporic plants found in the vicinity of Santa Monica. They are smaller and less profusely branched than the type material found at Pacific Beach, San Diego County. When more is known of it this may prove to be a distinct form.

Gelidium sinicola sp. nov.

Plate 47, figure 2

Fronds cylindrical to subcylindrical, 4.5–6 cm. high, less than half a millimeter in diameter, abundantly branched, with branches of 3–4 orders; color dark purple, almost black on drying; branches arising at wide angles, considerably contorted, not at all or only very slightly constricted at the point of origin, different orders varying but little in size, tapering abruptly to acute apices, subdistichous, irregularly placed, alternate, or in small part secund; cells in surface view very angular, irregularly placed, 6–8μ diam., elongated radially as seen in cross-section; medullary cells larger than the cortical, thick walled; rhizoidal filaments mostly among the medullary cells, sparse.

Growing in tide pools, in the middle littoral belt. Point Cavalo, San Francisco Bay, California, the type and only known locality. Type, Gardner, no. 2615 (Herb. Univ. Calif. no. 276620).

The species seems to be sparse and of limited distribution.

Gelidium densum sp. nov.

Plate 47, figure 1, and plate 48

Fronds 15–20 cm. high, up to 1 mm. diam., complanate, 1.5–3 times as wide as thick, the main branches being of almost uniform width from the base to near the apices, branches of 4–5 orders, the ultimate and subultimate ramuli often very numerous and densely congested, alternate or opposite, distichous, mostly only very slightly constricted at the base, blunt at the apices; tetrasporangia terminal on simple, longer or shorter ramuli according to position and age, frequently 1 cm. long; cystocarps and antheridia unknown; color dark pink; surface cells subspherical, 4–5μ diam. in surface view, arranged without special order; medullary cells densely congested with coarse granules; rhizoidal filaments moderately abundant, arranged mostly on the outer portion of the medullary tissue.

Growing in the sublittoral belt. Southern California. Type, Herb. Univ. Calif., no. 284086, contributed by the American Agar Company and collected at San Pedro, California.

I was unable to obtain much definite information concerning this species of *Gelidium*. It is apparently quite abundant but is rarely cast ashore. It was collected by the Japanese and used in the manufacture of agar agar at their factory in Glendale, California. The company is now known as the American Agar Company and is located in San Diego, where they are using large quantities of several species.

Gelidium ramuliferum sp. nov.

Plate 49

Fronds 25–30 cm. long, up to 1 mm. diam., ellipsoidal in cross-section; branches of several orders, groups arising in 4–5 zones, producing long, straight branches, the lower ones longest, those toward top reduced in length, all clothed with numerous short, wide-spreading ramuli; branches of all orders distichous, alternate or opposite; medullary cells very variable in size, congested with granules, up to 45μ diam.; tetrasporangia on the ends of relatively long, blunt, at times cordate, fructiferous ramuli; antheridia and cystocarps unknown; color dark red.

Growing in the sublittoral belt. San Pedro, California, the type and only known locality. Contributed by the American Agar Company. Type, Herb. Univ. Calif. no. 284027.

The type specimen of *Gelidium ramuliferum* is represented on plate 49. It is to be distinguished principally by the method of branching, well represented in this illustration.

Gelidium pulchrum sp. nov.

Plates 50–53

Fronds 15–20 cm. high, 300–500μ diam., almost cylindrical below, becoming gradually flattened toward the upper parts; branching distichous, of 5–6 orders, each order reduced in size, alternate or opposite, with relatively acute apices; cystocarps mostly single in the center of short, acute, fructiferous ramuli; tetrasporangia terminal on short, blunt ultimate ramuli; antheridia on longer ramuli quite variable in diameter in different parts; color purplish-red, usually fading to pink on drying.

Growing in the upper sublittoral belt. Southern California. Type, Gardner, no. 2569 (Herb. Univ. Calif. no. 295841). *Gelidium australe* Collins, Holden and Setchell, Phyc. Bor. Amer. (Exsicc.), no. 586.

This is a beautiful and rather slender species of *Gelidium,* purplish-red to pink in color. As far as is known at present, its distribution is limited to southern California. The type locality is Laguna Beach, Orange County.

This species on the Californian coast has passed under the name of *G. australe* J. Ag. I have compared our material with an apparently authentic specimen of this species from the herbarium of J. G. Agardh, now in the herbarium of the University of California, no. 93585, collected at Lacepede Bay, on the southern coast of Australia. This specimen is illustrated on plate 44. As may readily be seen, the branches of all orders are much more flagellate and tapering, closer together, more frequently opposite than in *G. pulchrum,* and are cylindrical throughout instead of being flattened.

Gelidium cartilagineum var. **robustum** var. nov.

Plate 54

Fronds long-stipitate, up to 7 cm. high, decidedly compressed throughout except the lower part of the stipe, up to 3 mm. diam. in the widest part, repeatedly and distichously branched, with branches mostly opposite but in part alternate; young branches standing almost at right angles at the base, geniculate, and the outer end almost parallel with the branch from which it arises, later all branches straightening and standing at about 45° angle; fructiferous ramuli short, blunt, and repeatedly branched; cystocarps usually single and below the center of ramuli, the outer ends of which are usually branched; tetrasporangia on the outer ends of much swollen ramuli with cordate apices; color brownish to purplish red, darker on drying, readily fading to pink on exposure.

Growing in the sublittoral belt. Central California to San Roque, Mexico. Type, Herb. Univ. Calif. no. 294572, collected near Ensenada, Lower California, and illustrated on plate 54.

Gelidium cartilagineum Collins, Holden, and Setchell, Phyc. Bor.-Amer. (Exsicc.), no. 135; Farlow, Anderson, and Eaton, Algae Exsicc. Amer.-Bor. no. 13; Collins, N. A. Alg. (Exsicc.), no. 162. I have not seen the specimen reported by Kylin (1925, p. 13) from San Juan Island, Washington, but probably it belongs here. If so, the range of the stated distribution is to be extended.

The specimens found in the northern part of the range are much smaller than those of the southern part. However, nothing is definitely known of the size except that gained from specimens cast ashore or found in the low-tide belt. The American Agar Company of San Diego uses this species principally in the manufacture of agar agar and has reported specimens nearly four feet long. It is very abundant on the coast of Lower California. Its southern limit of distribution has not been definitely made known. It is closely related to *Gelidium pacificum* Okamura, from Japan, a species apparently closely related to *G. cartilagineum*. The specimens here described from this side of the Pacific Ocean seem more closely related to *G. cartilagineum* than to the Japanese species, *G. pacificum*. I have therefore placed it as a variety of the former species.

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EXPLANATION OF PLATES

PLATE 36

Gelidium pyramidale sp. nov. A young, vigorous, tetrasporic plant, representing the type specimen.

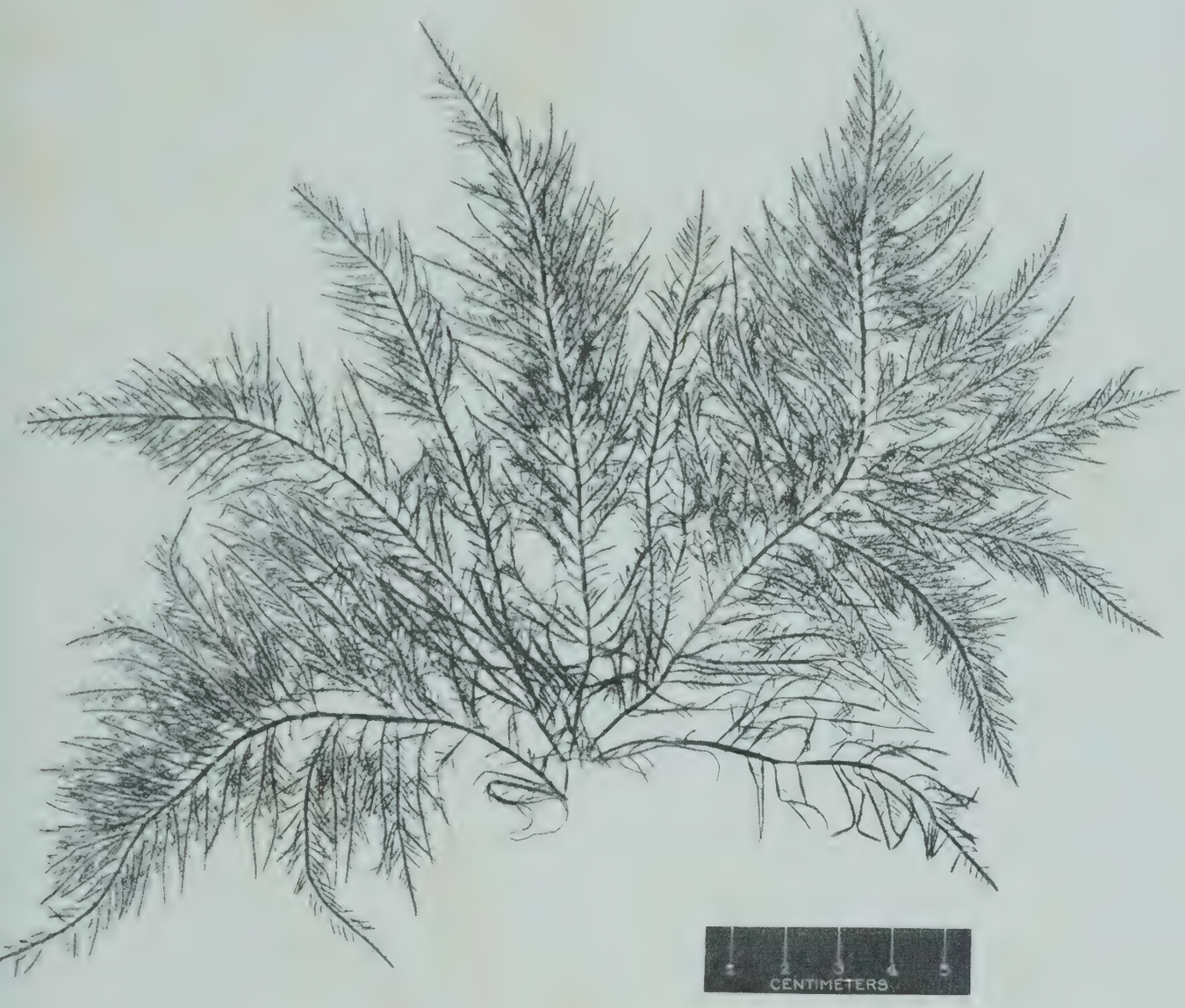
CENTIMETERS

PLATE 37

Fig. 1. *Gelidium pyramidale* sp. nov. A tetrasporic specimen, no. 585, *in* Collins, Holden, and Setchell, Phyc. Bor. Amer. × 0.8.

Fig. 2. *Gelidium nudifrons* sp. nov. Fragment of the type specimen of a cystocarpic plant. × 3.

Fig. 1

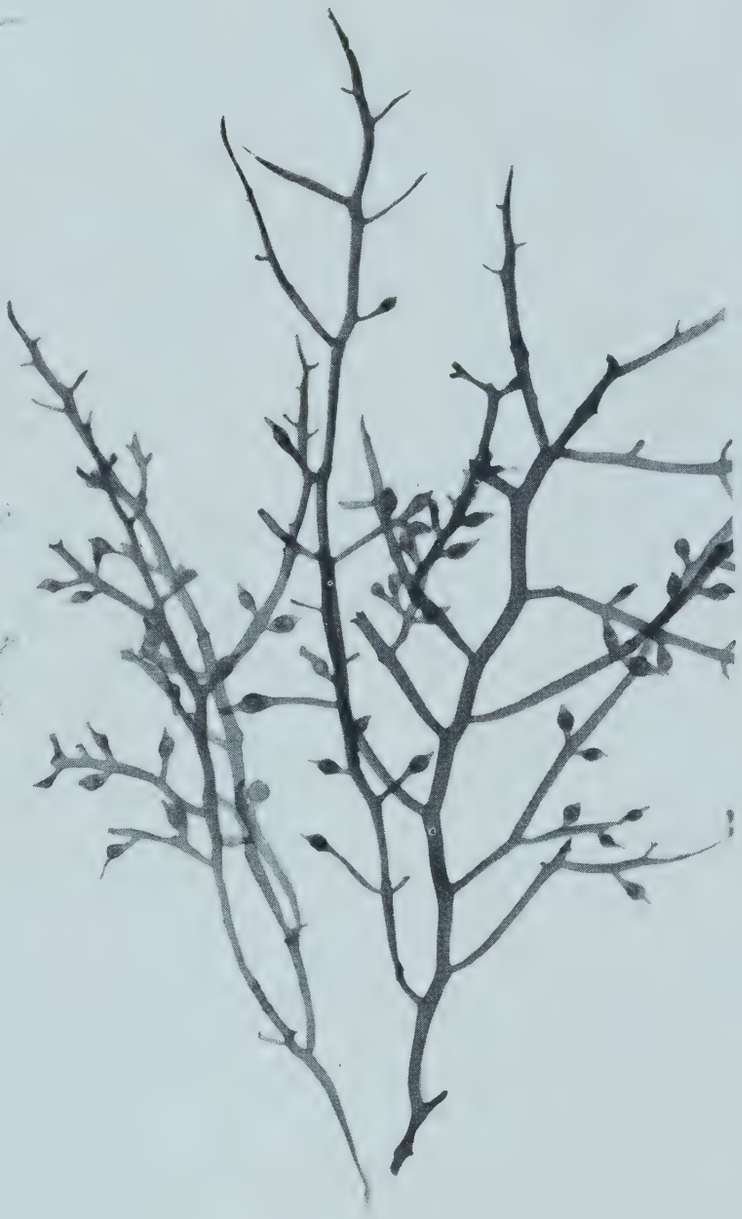

Fig. 2

PLATE 38

Gelidium purpurascens sp. nov. A tetrasporic plant. × 0.6.

PLATE 39

Gelidium purpurascens sp. nov. Fragments of a tetrasporic plant. × 3.

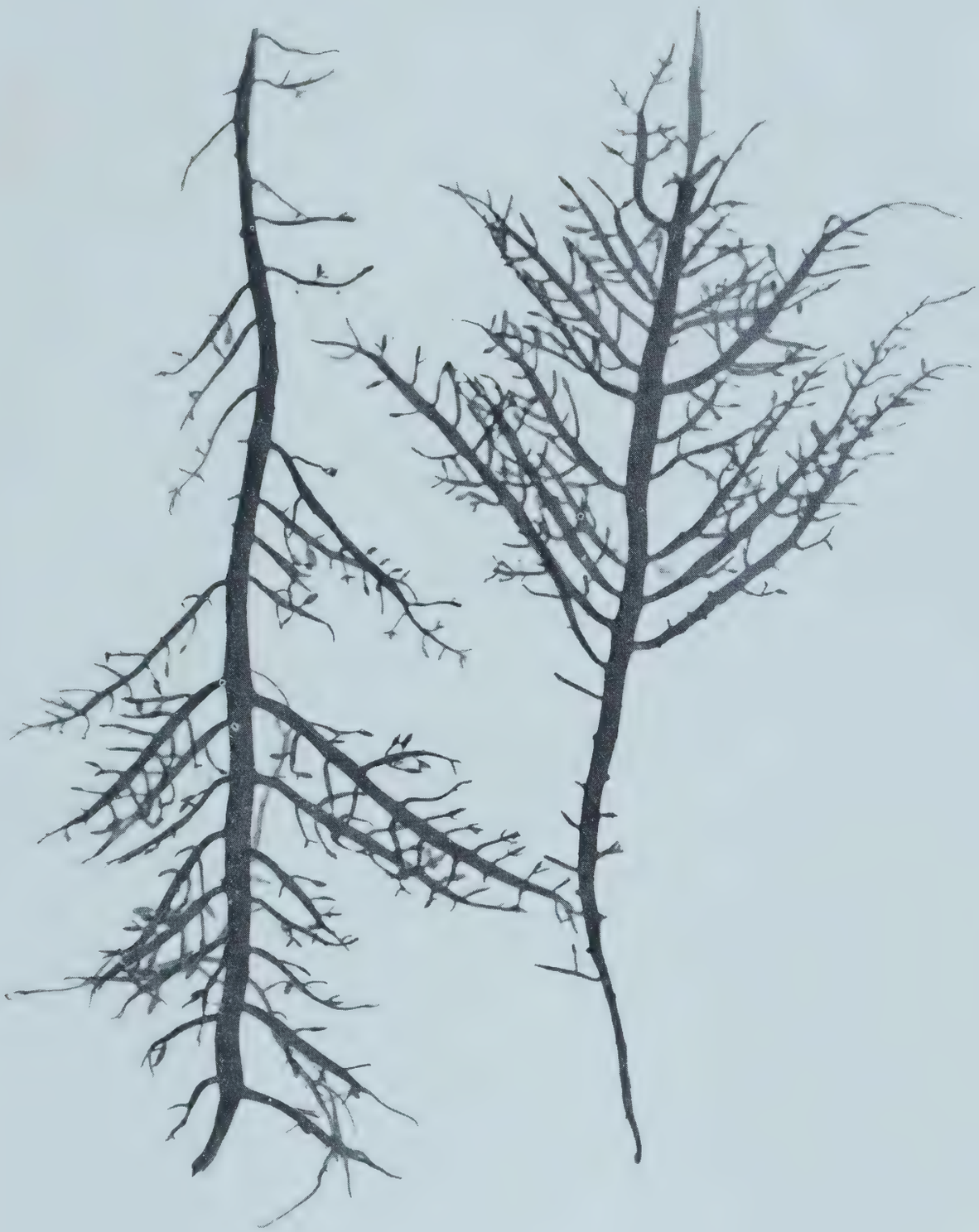

PLATE 40

Fig. 1. *Gelidium Setchellii* sp. nov. A cystocarpic plant, representing the type specimen.

Fig. 2. *Gelidium Setchellii* sp. nov. Fragments of a cystocarpic plant. × 3.

Fig. 1

Fig. 2

PLATE 41

Gelidium polystichum sp. nov. A tetrasporic plant, representing the type specimen. × 0.8.

PLATE 42

Gelidium arborescens sp. nov. A tetrasporic plant, representing the type specimen.

1 2 3 4 5
CENTIMETERS

PLATE 43

Gelidium nudifrons sp. nov. A cystocarpic plant, representing the type specimen. × 0.7.

PLATE 44

Gelidium australe J. Ag. An authentic tetrasporic plant (Herb. Univ. Calif. no. 93585). × 1.

PLATE 45

Gelidium pyramidale sp. nov. Several tetrasporic and antheridial plants, some sparsely and some densely branched.

CENTIMETERS

PLATE 46

Fig. 1. *Gelidium crinale* var. *luxurians* Collins. Fragment of a young tetrasporic plant. × 4.

Fig. 2. *Gelidium pyramidale* sp. nov. Fragment of an antheridial plant. × 3.

Fig. 1

Fig. 2

PLATE 47

Fig. 1. *Gelidium densum* sp. nov. A tetrasporic plant, moderately branched, representing the type specimen. × 0.7.

Fig. 2. *Gelidium sinicola* sp. nov. A tetrasporic plant, representing the type specimen. × 1.

Fig. 3. *Gelidium crinale* var. *luxurians* Collins. Several tetrasporic plants, representing the type specimens. × 1.

Fig. 1

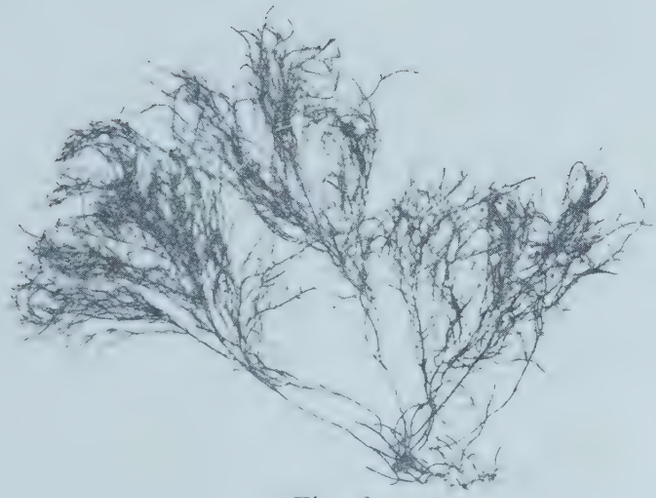

Fig. 2

Fig. 3

PLATE 48

Gelidium densum sp. nov. A tetrasporic plant, densely branched. × 0.8.

PLATE 49

Gelidium ramuliferum sp. nov. Representing the type specimen.

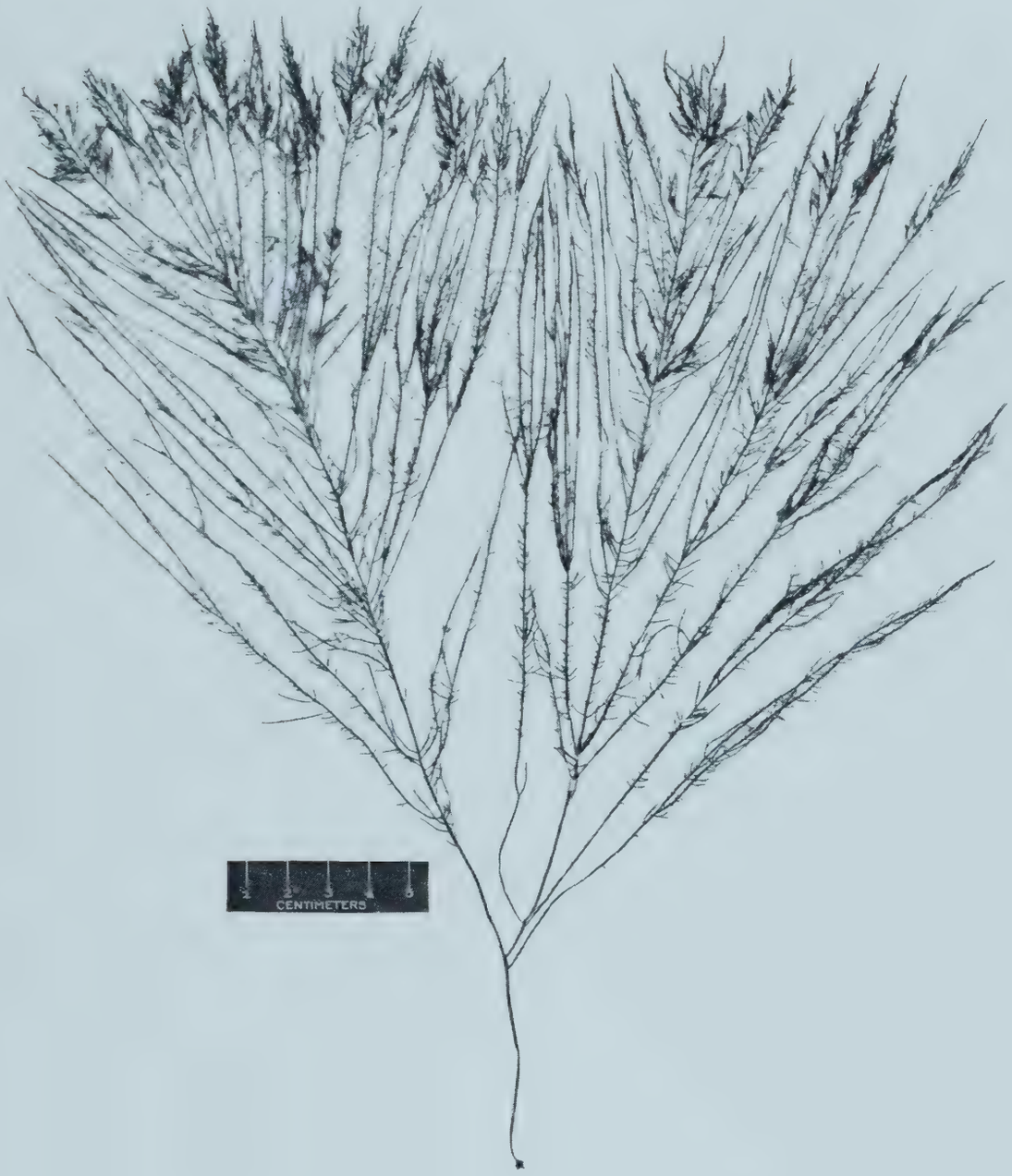
CENTIMETERS

PLATE 50

Gelidium pulchrum sp. nov. A relatively small, cystocarpic plant, representing the type specimen. × 1.

PLATE 51

Gelidium pulchrum sp. nov. Fragment of the type specimen, a cystocarpic plant. × 4.

PLATE 52

Gelidium pulchrum sp. nov. A relatively small, old plant, representing the type of a tetrasporic plant. × 1.

PLATE 53

Gelidium pulchrum sp. nov. Fragment of a tetrasporic plant. × 4.

PLATE 54

Gelidium cartilagineum var. *robustum* var. nov. A tetrasporic plant.

THE OCCURRENCE OF LATICIFEROUS VESSELS IN THE MATURE BARK OF HEVEA BRASILIENSIS

BY

EDUARDO QUISUMBING

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THE OCCURRENCE OF LATICIFEROUS VESSELS IN THE MATURE BARK OF HEVEA BRASILIENSIS

BY

EDUARDO QUISUMBING[1]

INTRODUCTION

In the course of examining slides of the sections of the bark of Para rubber trees the writer noticed certain anatomical features of the laticiferous vessels, which, though they may be present in trees in Malaya, Ceylon, Java, etc., seem to have been overlooked by earlier workers there; even Gandrup (1922) apparently does not mention them. The significance of these features to rubber work seems obvious.

The present contribution to the anatomy of the Para rubber deals primarily with the announcement that the laticiferous vessels occur outside, as well as within, the stone ring.

The earliest investigations of the distribution of the laticiferous vessels in Para rubber were made by Scott in 1884. Scott (1886) studied both 25-day-old seedlings and mature stems of *Hevea brasiliensis* and endeavored to compare the nature of the laticiferous vessels of *Hevea spruceana* with those of *Hevea brasiliensis*. He noticed a hypodermal system of laticiferous vessels in *H. spruceana* but not in *H. brasiliensis,* at any rate in the hypocotyledonary stem and the first epicotyledonary internode. Scott stated that the laticiferous vessls in embryos occurred on the phloem side of all the bundles, none occurring in the parenchyma between the bundles, and that they were abundant in the cotyledons of the germinating seeds.

Miss Calvert (1887) found a small number of laticiferous vessels in the pith of *Hevea* seedlings 21 to 25 days old and observed that the vessels of the pith and the cortex communicate with one another at the nodes. Medullary laticiferous vessels were found also to occur in older seedlings. She observed that in the upper part of the older

[1] Research Associate in Botany, University of California, Assistant Professor of Plant Physiology, College of Agriculture, University of the Philippines, on leave. This work was undertaken at the suggestion of Dean C. F. Baker.

seedlings the laticiferous vessels in the hypodermis or outer cortex seem to arise as branches. Branches from these vessels were frequently found running obliquely upward through the cortex, passing between the elements of the sclerenchyma sheath and continuing their course in the hypodermal tissue. Hypodermal laticiferous vessels were found by Miss Calvert only in the upper half-inch of the first internode of the epicotyl and in the succeeding short internodes. She found hypodermal vessels in seedlings only, reporting none in the bark of the mature trees. Arens (1911) noted the occurrence of laticiferous vessels in the pith of *Hevea* trees and stated that there is no connection between neighboring rows of laticiferous vessels in the cortex. Johnson (1909) mentioned that the majority of laticiferous vessels in the trunk of the trees are situated in the tissues between the bark and the wood, and that in contrast to those observed by Miss Calvert, which run obliquely, these traverse the bark principally in a longitudinal direction, with very little lateral communication. Petch (1911) remarked that, in the stem of the seedling after germination, laticiferous vessels are found in the pith, and these are continuous with the laticiferous vessels in the cortex, at the nodes. He mentioned their occurrence in the leaves. Bryce and Campbell (1917) reviewed the previous work on the anatomy of Para rubber and investigated the variation in the number of rows of laticiferous vessels at different seasons and at various heights in the same tree. They remarked that in the outer layer of the cortex the laticiferous vessels could no longer be detected and that connections between neighboring rows of latex vessels were not observed. These investigators noted cases of bifurcation of rows. Brown (1918) states that the cortex of mature *Hevea* trees contains numerous laticiferous vessels which run in a longitudinal direction, and that they are most numerous in the inner layers of the cortex near the cambium, where they are arranged in series of concentric rings encircling the stem, and where they form a complex network by reason of their lateral communications. Bryce and Gadd (1922) considered the cortex to comprise three latex vessel zones, (*a*) a zone of continuous latex vessel rows in the inner cortex, (*b*) a zone of interrupted rows, (*c*) a region of scattered fragments, the transition points being usually ill defined. Gandrup (1922) states that no laticiferous vessel was found outside of the stone ring.

Up to the present, however, there is no record, so far as I know, that laticiferous vessels have been found outside of the stone ring, in mature trees of *Hevea brasiliensis*.

MATERIAL AND METHODS

The two thousand seeds from which some of these plants were raised, were received from J. D'A. Pereira, Singapore, on December 22, 1910. These seeds were collected, according to records, from trees 10 to 12 years old. The seedlings were transplanted to the field on February 6, 1911.

Pieces measuring 3 × 2 cm. were cut from the bark of these trees at 30 cm., 60 cm., and 90 cm. from the ground. The sections were immediately fixed in the field in acetic-formalin-alcohol, and left in the fixing agent for 48 hours before cutting. Transverse and longitudinal sections of 10 to 15 micra of the bark were made on a sliding microtome. These sections were then placed in 50, 70, and 80 per cent alcohol. Sections were stained with Flemming's triple stain, which was found to be very satisfactory. After staining, the sections were dehydrated, cleared, and mounted in Canada Balsam.

DISTRIBUTION OF THE LATICIFEROUS VESSELS

To understand clearly the structure and the distribution of the laticiferous vessels, it is necessary to consider first the general structure of the mature stem. We may divide the stem, conventionally, into bark and wood. All the tissues outside of the cambium constitute the bark, and those within belong to the wood. The bark may be further differentiated into outer bark and inner bark. The outer bark comprises the phellogen and the cork cells. The inner bark consists of the outer bast and the inner bast (pl. 55). The inner bark is the tissue *par excellence*, from the point of view of the producer and the tapper.

As noted above, all investigators have observed laticiferous vessels both in seedling stages and in mature trees. They occur in the pith in seedlings and in the apices of the young twigs. As the seedling gets older laticiferous vessels decrease in number in the pith until finally none are seen. In the seedling and in the apex of the mature stem, as well as in the bark, the origin of laticiferous vessels is clear. At first a single cell undergoes transformation, later neighboring cells follow suit, so that eventually we have either a single tube formed by a row of cells, or branching tubes, due to the absorption of the lateral walls

by adjacent cells or tubes (pl. 58, figs. 1–2). In the young seedlings and in young twigs the laticiferous vessels are more or less centripetal, but as the seedling gets older and we proceed downward to the twig, the laticiferous vessels are found to assume a parietal position as they approach the xylem ends.

In young stems, before the cambium ring is developed, the laticiferous vessels are scattered in the cortex, outside the pericycle. The laticiferous vessels in young stems and in the hypodermis were never found as branches or blind ends, an observation not in accordance with the findings of Miss Calvert (1887). They have also been uniformly observed in the medullary rays and are undoubtedly of cambial origin. That they communicate with the cortex is hardly conceivable, since the cambium acts as a limiting factor.

From the base of the trunk upward, the number of rows and of individual laticiferous vessels decreases. This is a further indication that the majority of laticiferous vessels are of cambial origin; all except those found in the outer bast, which are of cortical and phellogenetic origin. Branches of laticiferous vessels are present, the greater number being parallel to the axis of the tree, but some of them oblique.

The two current views regarding the origin of laticiferous vessels are, one, that the laticiferous vessels in the secondary cortex are produced solely by the cambium; two, that the vessels are formed *de novo* in the cortex by the absorption of the walls of the ordinary cortical cells. According to the observations of the writer, both types of origin occur in the Para rubber tree. While the cambium ordinarily may give rise to cells producing laticiferous vessels, any cells of the primary cortex and cells produced centripetally by the phellogen may be transformed into laticiferous vessels, and this is particularly true in the case of the laticiferous vessels outside of the stone ring (pls. 56–57).

Connections of laticiferous vessels at the nodes between pith and cortex were observed by Scott (1886) and Miss Calvert (1887). The writer found this to be true in the case of nodes, but failed to see such connections in the internodes.

In mature trees, laticiferous vessels occur both in the roots and in the leaves, but less abundantly in the latter. The presence of the laticiferous vessels in these organs is obviously not of commercial importance.

Inasmuch as we are concerned particularly with the stem of the mature tree, we will now consider the nature of the laticiferous vessels in the mature bark. While laticiferous vessels occur throughout the

bark, including the region outside of the stone ring (pls. 56–57), the chief seat of their occurrence in the trees studied is the region between the cambium and the stone ring; many more are found in the inner bast than in the outer bast. This difference is due to the fact that more stone cells, which interfere with the formation and ramification of laticiferous vessels, are present in the outer than in the inner bast (pls. 56, 57, and 58, fig. 3). There are individual stone cells and groups of stone cells in the inner bast also, but the number there is much smaller (pl. 58, fig. 2). This is true both of shaded trees and of trees located in the open. The laticiferous vessels ramify, and often the branches fork dichotomously (pl. 58, fig. 1).

All the trees on the campus of the College of Agriculture at Los Baños exude latex when the bark is scratched. This has been a puzzle to some, but the explanation is indicated above, namely, that there are laticiferous vessels outside of the stone ring. In this region outside of the stone ring, one may confuse tanniferous cells present with laticiferous vessels. But tanniferous vessels are more or less localized and only found associated with the cork cells, or near them. Microchemically, tanniferous vessels may be distinguished from the laticiferous vessels, as the latter cannot be macerated with dilute KOH solution. In addition, one can readily distinguish the laticiferous vessels from the tanniferous cells by their length, by their anastomosing features, by their contents, and by the structure of the walls. The tanniferous cells are never more than one cell long, whereas laticiferous vessels are generally made up of several cells. Both laticiferous vessels and tanniferous cells take safranin equally well, but the tanniferous cells absorb it more easily.

The anastomosing network of laticiferous vessels is evident in the case of the tangential sections of the bark, both from the region of the inner bast and from the outer bast (pl. 58, figs. 1–2). Near the phellogen they do not branch so freely (pl. 58, figs. 3–4).

In many cases it was observed that the partitions and septae completely disappear at the maturity of the laticiferous vessels, but in some cases a vestige of the septa remains. Some of the laticiferous vessels continue to ramify and communicate with neighboring vessels by a bridge tube (pl. 58, fig. 1); other branches are blind and end abruptly.

It has been reported from Ceylon that the region of maximum occurrence of laticiferous vessels is deep-seated and nearest the cambium, whereas, from the Straits Settlements, the laticiferous vessels

are reported not to be deep-seated. Therefore, in Ceylon it was found necessary to tap deeper to reach the region of most abundant latex flow. As shown above, in the Philippines as in the Straits Settlements the region of greatest flow is not deep-seated. It is in the inner bast, some distance outside the cambium. In addition, in the Philippines, peripheral laticiferous vessels occur in the mature bark. The occurrence of a less deep-seated region of flow is of decided advantage in tapping and serves as a criterion of selection.

SUMMARY

I. Laticiferous vessels occur in the pith in young stems and in seedlings, in the leaves, and also in the roots.

2. No latex tubes are found in the secondary wood, but some are found in the medullary rays.

3. In the bark, laticiferous vessels are abundant in the inner bast. Some are found in the outer bast, and in the region outside of the stone ring, but they do not branch so freely as those in the inner bast.

4. Latex tubes may have two origins in the mature bark, one of cambial origin in the secondary cortex, within the stone ring; and the other of peripheral origin, outside of the stone ring, coming from the primary cortex and phellogen.

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EXPLANATION OF PLATES

All figures photomicrographed by the Bureau of Science, Manila, using C Zeiss AA objective, and compensating ocular No. 4.

The following abbreviations have been used on the figures: *c.*, cambium; *c.c.*, cork cells; *b.*, inner bark; *b'.*, outer bark; *i.b.*, inner bast; *l.v.*, laticiferous vessels; *o.b.*, outer bast; *p.*, phellogen; *s.c.*, stone cells; *s.r.*, stone ring; *t.c.*, tannin cells.

PLATE 55

Transverse section of the bark including a portion of the cambium, showing cork cells, phellogen, stone ring (not very clear here), outer bast, inner bast, outer bark, inner bark, stone cells. × 90.

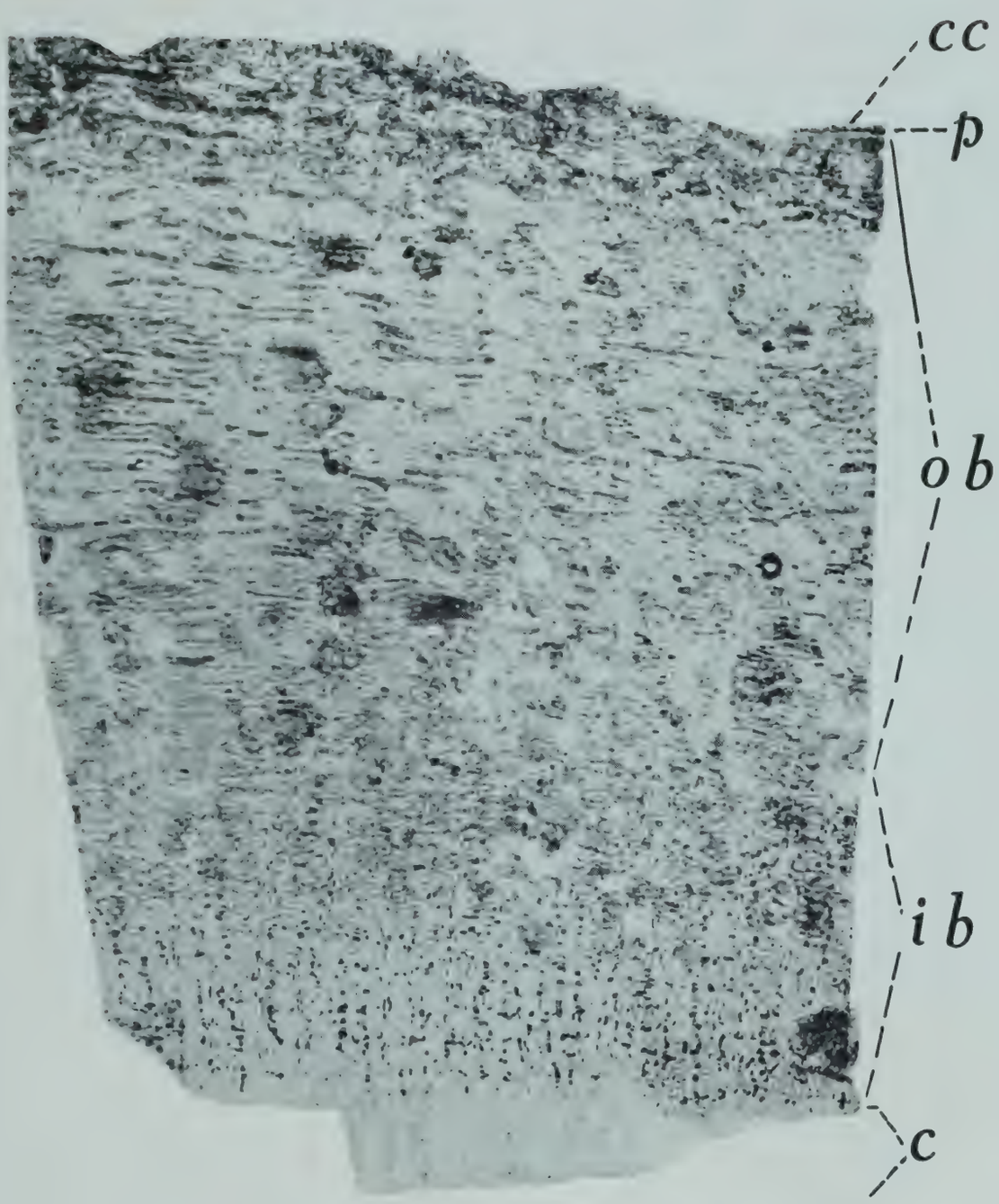
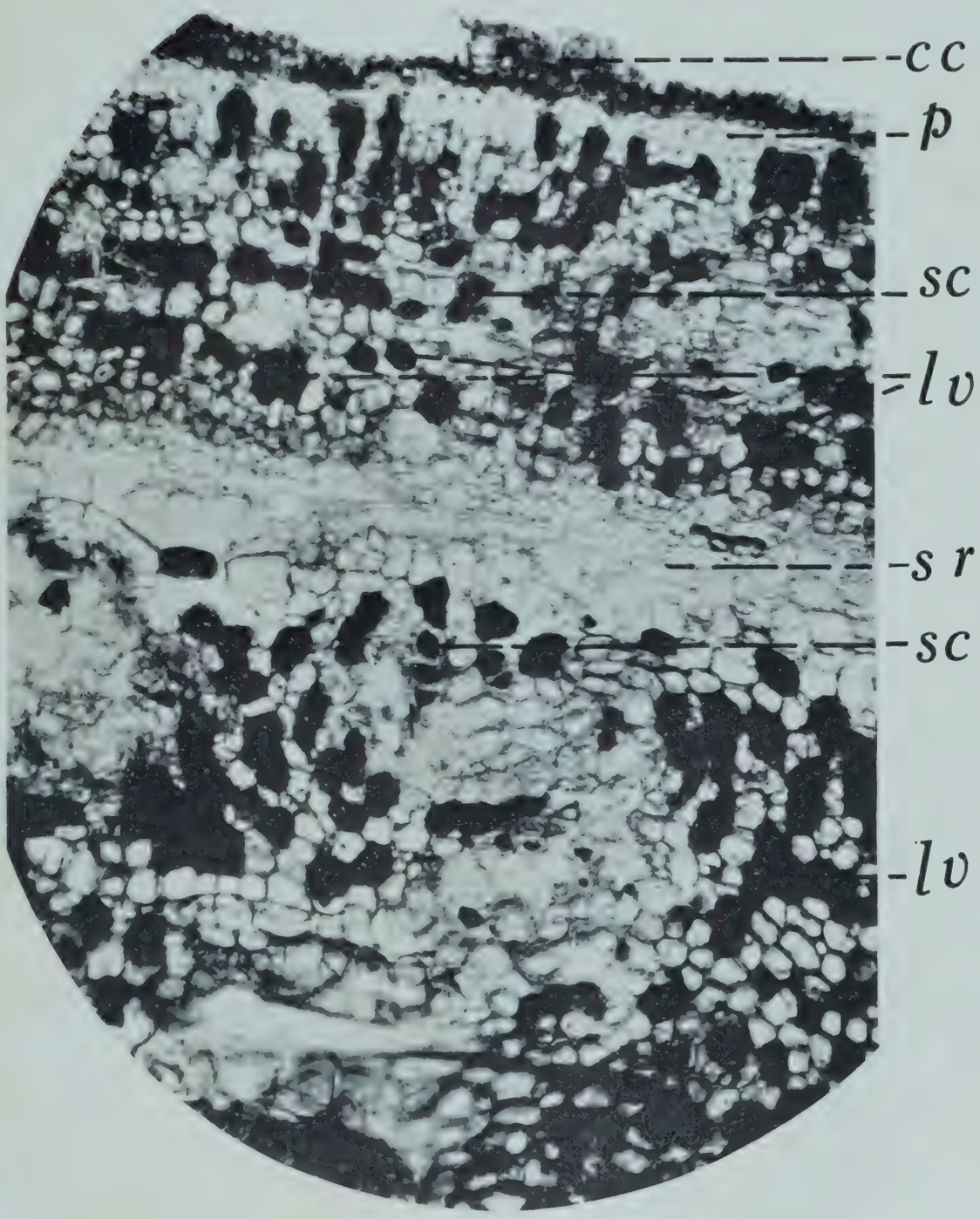

cc
p
ob
ib
c

PLATE 56

Transverse section of the bark showing laticiferous vessels outside of the stone ring. × 600.


cc
p
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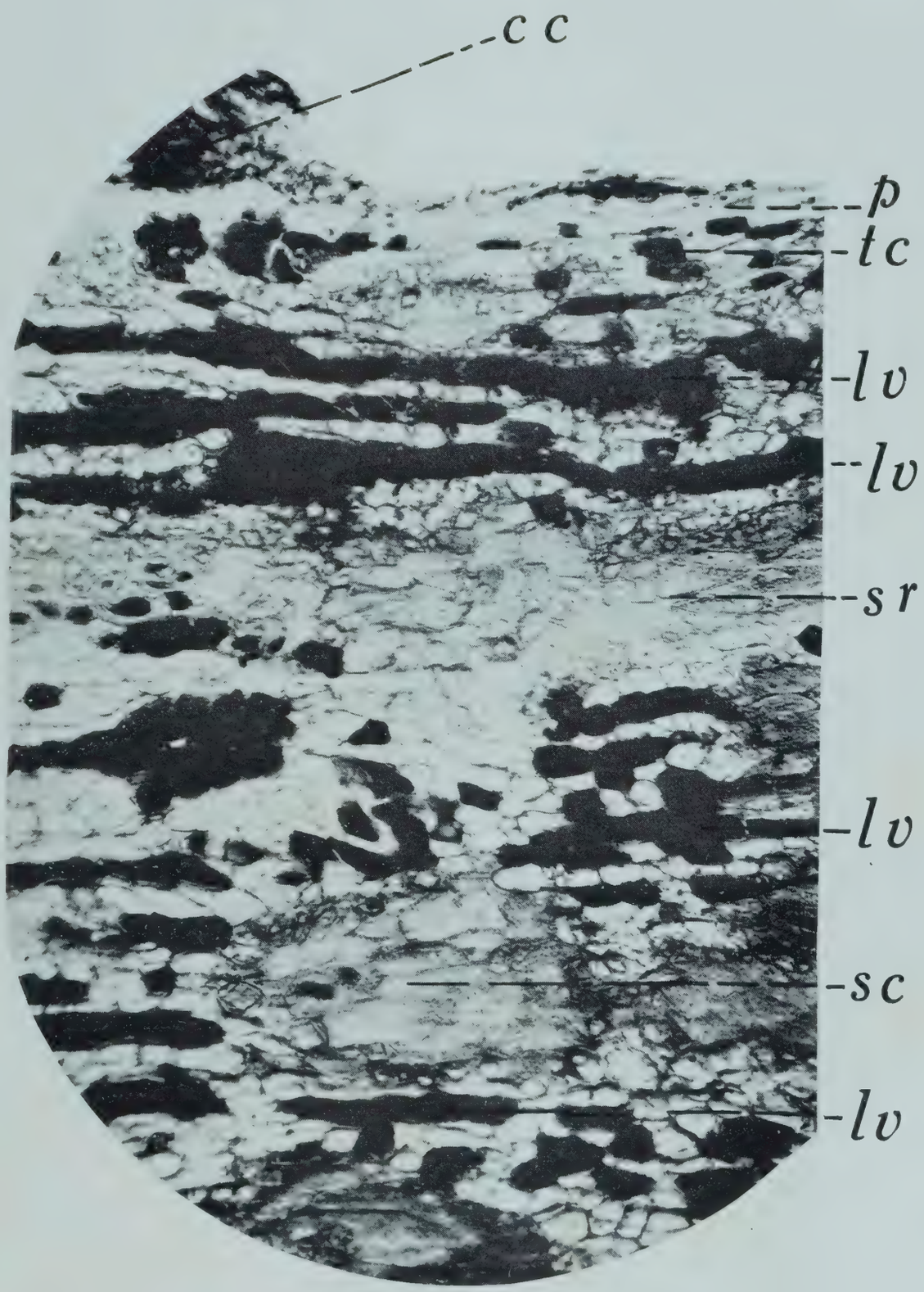
sr
sc
lv

PLATE 57

Radial section of the bark showing the nature of the laticiferous vessels outside of the stone ring and tannin cells. × 600.


cc
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tc
lv
lv
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lv
sc
lv

PLATE 58

Fig. 1. Tangential section of the bark showing the nature of the laticiferous vessels in the middle region between the inner bast and the outer bast. × 300.

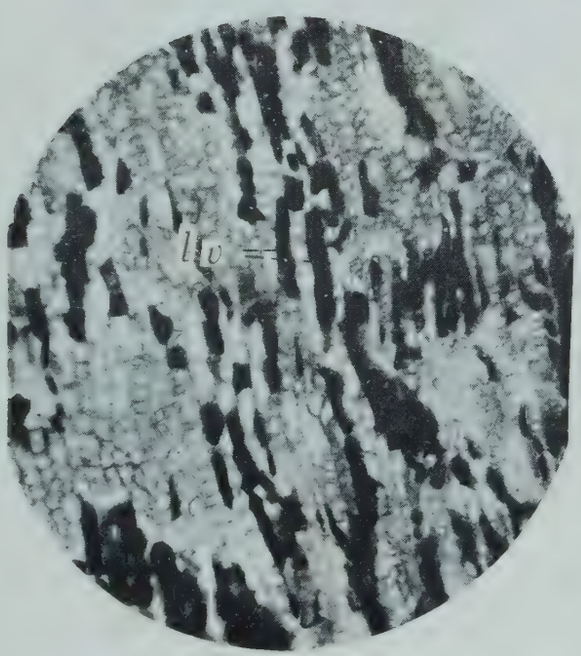
Fig. 2. Tangential section of the bark showing the nature of the laticiferous vessels in the region near the cambium (inner bast). × 300.

Fig. 3. Tangential section of the bark showing the nature of the laticiferous vessels in the region within the stone ring (outer bast). × 300.

Fig. 4. Tangential section of the bark showing the nature of the laticiferous vessels in the region between the stone ring and the phellogen. × 300.

l.v
l.v
l.v

s.c
l.v


l.v

l.v
s.c

5417